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Heart Rots in Living Trees.
WILLIS W. WAGENER AND ROSS W. DAVIDSON 61

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HEART ROTS IN LIVING TREES

WILLIS W. WAGENER AND ROSS W. DAVIDSON[1]

Introduction 61
The Fungi Causing Heart Rots 64
Dissemination of Heart-rot Fungi 66
Nuclear State of Heart-rot Fungi 67
Establishment of Heart Rots 68
Nature of the Decay Process 75
Stages of Decay 76
Types of Heart-rot Decay 77
Progress of Heart-rot Fungi in Trees 80
Progess of Decay in Individual Trees 80
Progress of Decay in Stands 85
Conditions Influencing Progress of Decay in Individual Trees 89
Effect of Gases 89
Effect of Moisture 91
Effect of Temperature 91
Effect of Wood Characteristics 93
Effect of Infiltrated or Deposited Materials 95
Conditions Influencing Progress of Decay in Stands 98
Age of Stand 98
Stand History 100
Stand Composition 101
Site 103
Physiological Effects of Heart Rots on the Host 107
Estimation of Decay in Living Trees 108
Losses from Heart Rots 111
Avoidance or Reduction of Heart Rots 114
In Forest Trees 114
In Orchard and Shade Trees 118
Literature Cited 119

INTRODUCTION

Tree trunks beyond the sapling stage typically consist of cylinders of living wood, the sapwood, protected on the outside by bark and surrounding a central core of physiologically dead wood, the heartwood. The living white sapwood, which may comprise from 1 or 2 up to as many as 100 to 200 growth rings in different tree species (48), ordinarily is resistant to decay as long as it remains alive and uninjured and serves to protect the underlying heartwood

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from invasion by decay fungi. However, this protective layer does not remain intact indefinitely. With age, various openings are formed through which heart-rot fungi may enter.

Any decay that becomes progressive in the central dead wood of a living tree may be termed a " heart rot ", as distinguished from decays primarily of the sapwood, referred to as " sap rots ". However, some sapwood-rotting organisms, such as *Fomes pinicola* (88, 158) and *F. applanatus* (327), may also cause heart rots, and a few wood-rotting fungi, among them *Ustulina vulgaris* (66, 331), *Fomes lignosus* (120), *Irpex mollis* (272) and *Polyporus hispidus* (297), are able to attack both heartwood and living sapwood after they have become established in a susceptible host.

Trees of all kinds and sizes, from the giant redwoods (117) of the California coast to the short spruces and birches of the arctic regions (26), the bushy xerophytes of the semi-arid Southwest (201, 289), and even small woody shrubs (92, 93) are subject to heart rots. Likewise, some of the larger cacti may suffer rots of the woody skeleton (93) similar to those of the heartwood of our more conventional trees. This wide range of hosts suggests that the heart rots are not a recent development in point of time in the earth's history, an inference borne out by paleobotanical records. Although a number of early reports of polyporaceous fossil sporophores have been discredited (183), several authentic specimens are known from Pliocene strata in Germany and the western United States (4, 50, 182, 183), indicating that heart-rotting fungi were well established in the late Tertiary. Decayed coniferous wood has been found in formations as early as the Jurassic in Germany (183). A fruit-body of a heart-rotting fungus, *Fomes applanatus,* from the Pleistocene of California has been judged not to differ from modern examples of this species and probably affected the same host, *Umbellularia californica,* as it commonly does in that region today (212).

Black locust, osage orange, Douglas-fir, redwood and most species of pine, oak, cherry, cypress, hemlock, spruce, walnut, juniper and cedar (*Thuja* and *Libocedrus*) develop what may be called a true heartwood, darker in color than the sapwood and differing from it in both chemical and physical characteristics. In these species the sapwood remains relatively thin, in many not more than an inch in width, and changes quite regularly, as new wood is added on the outside, into heartwood on the inside. In others, such

as in the elms, hickories, apple, ash, some of the maples and pines, and in the true firs, the change occurs later on the average, often resulting in a much thicker sapwood, and is more irregular, not only within individual trees but between different trees of the same species. In consequence, trees of the same age may show wide differences in the percentage of sapwood.

In some species, as in basswood, European beech and spruce, the heartwood appears little different from the sapwood except for the absence of living tissues and the accompanying lowered moisture content. These are termed " ripewood trees " by Büsgen et al. (59) who distinguish still another group, designated as " sapwood trees ", in which there is no readily visible differentiation between heartwood and sapwood. Alder, aspen and birch are examples of this group.

The change from sapwood to a pronounced heartwood in the tree species for which this is characteristic is accompanied by the formation and deposition of various substances, including oils, resins, gums, tannins, dyes and organic salts, which determine the color of the heartwood and also its particular physical and chemical properties. These substances are infiltrated into the cell walls or, when abundant, may be deposited in an amorphous form within the cell cavities (48) or in the intercellular spaces. In the hardwoods they may also be laid down in the form of tyloses in the wood vessels. Their nature and identity vary not only with different families of trees but also between species, and even varieties. Many of them are extractable in hot or cold water (137) or other solvents, and of these a number have been shown to be toxic to various wood-rotting fungi used as test species (3, 102, 104, 247, 299, 340). These toxic extractives undoubtedly are major factors in determining the relative durability in service of the heartwoods in which they are present. A water-and-alcohol-soluble extractive, fungistatic to the decay fungus, *Schizophyllum commune,* recently has been reported in the heartwood, sapwood and bark of living *Catalpa speciosa* (208). It disappears soon after the death of the tissues and is probably present in the heartwood only through diffusion from the living sapwood. The discovery of this transient extractive in catalpa suggests that similar ones may occur in living trees of other species and may aid in their protection. However, regardless of the character and content of deposited or diffused compounds, the heartwood of practically every tree species is subject

to decay in the living tree by one or more heart-rot fungi adapted to growth there.

In addition to the great diversity in infiltrated substances, heartwood differs widely in permeability to liquids (164) and in moisture content; but, just as various heart-rotting fungi are adapted to development in the presence of specific heartwood constituents, so are particular ones adjusted to growth within different ranges of moisture content, some high and some low. In elms, poplars and a number of other genera of trees, an abnormally moist condition of the heartwood, or of a zone at its outer edge, known as "wetwood" or "water wood", is quite common (83, 86, 190). The water-soaked wood almost invariably registers higher in pH than normal wood, contains associated bacteria or yeast-like fungi (62, 83, 86), and in elm has been attributed definitely to the presence of a bacterium (71). Former wetwood sometimes is mistaken for incipient decay.

With few exceptions, heart rot fungi, when once established in trees, have little effect on the surrounding sapwood, but they may progress into the heartwood of branches and into branch stubs. Thus trees with heart rot may appear quite healthy, even though structurally weakened, and if not subjected to undue mechanical strains, such as those from storm winds or from ice formation, may stand intact for many years.

THE FUNGI CAUSING HEART ROTS

Most of the thousands of fungi capable of producing decay in wood are Hymenomycetes of the families Polyporaceae (204, 205, 235, 293), Thelephoraceae (58), Hydnaceae (220) and Agariaceae (177). A few, such as *Ustulina vulgaris* (66), may be Ascomycetes. Of these thousands, only a relatively few, probably not over several hundred, are able to develop in and decay the heartwood of living trees, and a few are active only there. Some, such as *Fomes pini* and *Polyporus schweinitzii* in coniferous hosts, and *Polyporus dryophilus* and *Fomes robustus* in broad-leaved species, are world-wide in distribution. A few, exemplified by *Polyporus sulphureus* and *P. dryadeus,* are known to cause heart rots in both softwoods and hardwoods. Others are restricted to single or to very limited host species, such as *Polyporus amarus* in incense-cedar and *Poria sequoiae* in redwood.

In the past, the common basis for judging the identities of heart rots and their causal fungi has been through the association of sporophores with the decays on live trees, or their association with decays of similar appearance. In very few cases have the judgments been supported by experimental proof through isolation of the causal fungus, its implantation into sound heartwood and reproduction of the decay in the latter. Investigations, in which attempts have been made to isolate the causal fungi from all cases of decay found in the trees of a study sample, have shown that many fungus species are active which previously were not known to cause decay. A large number of fungi were found to be of some importance as causes of decay in oaks in the eastern United States (91), and several other decay-producing species, which had not been found in the original study, were later encountered (68, 92). It seems quite probable that further studies in oak forests, especially in other areas, will disclose additional heart-rot fungi associated with decay of oaks. Preliminary studies in other forest types, such as hardwoods, in the northern United States (61, 63, 65, 66, 69, 88, 90) indicate that further investigation and use of the isolation method for confirmation of the identities of fungi responsible for the decays encountered will continue to disclose many not previously known to be associated with heart rots of the various hardwood hosts. In conifers, also, our knowledge of decays is still quite incomplete in many parts of the world, as indicated for western North America by the work of Canadian investigators (28, 30, 31, 32, 33, 51, 53, 54, 95*a*, 111, 112, 112*a*, 257*a*, 308*a*, 328*a*), that of Englerth (99) and of Rhoads and Wright (257). Baxter and associates (24, 25, 26) have added much to our knowledge of Alaskan heart rots.

A striking recent example of the value of the cultural method in correcting earlier information on decays in a conifer species is provided by the work of Basham, Mook and Davidson (19). By this means they were able to show that white stringy butt rot of balsam fir is chiefly caused by *Corticium galactinum* and *Odontia bicolor*, not by *Poria subacida*, as reported in most earlier publications, and that other decays, previously unreported for the species, were present. On the other hand, Thomas and Podmore (308*a*) found that in black cottonwood the usefulness of the cultural method was limited because of bacterial contaminants in the affected wood.

Among the important contributions in recent years on the occur-

rence and identity of heart rots in parts of the world outside North America have been those of Cartwright and Findley (75, 77) and Peace (238) in the British Isles; Björkman et al. (36), Jørstad (170), Jørstad and Juul (171), Kangas (172*a*), Rennerfelt (254) and Roll-Hansen (269) in Scandinavia; Fröhlich (118), Kalandra and Pfeffer (172), Krstic (187), Pinto-Lopes (242, 243), Rohmeder (267) and Schober and Zycha (287) in central and southern Europe; Ankudinov (7), Bondartzev and Liubarskii (38) and Murashinskii (229) in Russia and Siberia; Bagchee (12*a*), Bagchee and Bakshi (13), Bakshi and Bagchee (13*a*) and Banerjee and Bakshi (14) in India; Hussain (164*a*, 164*b*) in Pakistan; Teng (307) in China; Aoshima (9, 11), Hemmi and Akai (141) and Imazeki (165, 166, 167) in Japan; Parkin (237) and Tamblyn (306) in Australia; and Birch (34) in New Zealand.

DISSEMINATION OF HEART-ROT FUNGI

Characteristically, transfer of heart-rotting fungi from tree to tree is by means of spores which are produced by the organisms on specialized fruiting structures, the sporophores, the more evident of which are commonly referred to as " conks ". They are of various shapes from a plain hyphal crust over the surface of wood or bark to large imbricate or hoof-shaped bodies, and on living trees they usually emanate from knots or the exposed wood of wounds, or appear on the bark of dead trees. Those of a few butt and root-rotting fungi may push through the soil around the base of affected trees. Sporophores may also be produced on the trunks, down logs and stumps of dead trees or on dead limbs and branches.

Basidiospores, which vary in shape from globose to cylindric and average about five microns in diameter, are liberated from the hymenium of the sporophore over periods of from a few days, as in *Armillaria mellea* (56) and *Trametes suaveolens* (155), to six months or more, as in *Fomes applanatus* (327). The numbers produced are sometimes enormous, ranging from approximately 260 million per day for a medium-size sporophore of *Fomes igniarius* (55) to 30 billion per day from a fairly large fruit body of *Fomes applanatus* (327) and over 300 billion per day from one of *Fomes fomentarius* (52, 153). Individual basidiospores are so light that they are little influenced by gravity and, because of the normal conditions of air turbulence in the open, may be considered

as in suspension in air rather than as particles falling under gravity (131). After release from the sporophore the numbers of spores present in the air decrease rapidly with increasing distance from the point of liberation because of dispersion and interception (131, 332, 333); but, because of their lightness and the enormous initial numbers, some of the spores undoubtedly are carried great distances during windy periods. They may also be carried from tree to tree by insects, birds, man or other animals such as rodents (161).

Many heart-rot fungi produce only basidiospores, but a number also form secondary spores (13, 47, 91, 92, 174, 231), and a few, such as *Ptychogaster cubensis,* normally have only a conidial stage (92). Among those which produce conidia or chlamydospores in great abundance are *Polyporus balsameus, P. compactus, P. guttulatus, P. sulphureus* and *Fomes laricis. Fomes annosus* forms conidia abundantly on laboratory media but rarely in nature, according to Rishbeth (260), and he believes it unlikely that they play an important role in the dispersal of the fungus. Little is known about the place of conidia in the dissemination of other heart-rot fungi.

Some decay fungi commonly grow on roots, and these may spread not only by means of spores but also by the growth of mycelium through the soil to the roots of uninfected trees or across contacts between infected and sound roots. Specialized organs for such spread are the rhizomorphs produced by a number of wood-destroying fungi (120, p. 19) and composed of dense aggregates of fungus hyphae. It is possible also that oidia, other secondary spores and fragments of living mycelium or of wood containing viable mycelium may be carried from tree to tree by woodpeckers or insects, although Leach et al. (191), in a study of the development of decay in freshly felled red pine logs, concluded that the insect invaders were not concerned in introducing the decay fungi that became established in the logs.

NUCLEAR STATE OF HEART-ROT FUNGI

The mycelium of most established infections of heart-rot fungi that have been investigated has been found to be diploid, with paired nuclei, and exhibiting clamp connections that demonstrate it to be heterothallic. However, some heart-rotting species, such as

Stereum sanguinolentum, as reported by Robak (264), are apparently characteristically homothallic, with haploid nuclei. Heterothallic species may be either bipolar, with spores of two different pairing types produced on each fruit-body, or tetrapolar, with four pairing types (57, 329). From a survey of most investigations to date, Whitehouse (329) concluded that, from the sample of species represented and considering the Hymenomycetes and Gasteromycetes as a whole, ten per cent are homothallic, 35 per cent heterothallic and bipolar and 55 per cent heterothallic and tetrapolar. The literature for the Hymenomycetes has also been reviewed by Quintanilha and Pinto-Lopes (247*a*). Owing to the facts that a single germinating spore produces only haploid mycelium and that most isolations from decay cases are found to be in the diploid condition, the assumption can be made that these have resulted from multiple-spore infections. Haploid mycelia of decay fungi are able to produce decay in wood but usually at a slower rate than those in the diploid state (176, 265, 317).

Employment of haploid monosporous cultures in interfertility studies has proved to be a very useful tool in the segregation of decay organisms with similarities likely to cause confusion and in the delimitation of species. A particularly good example is the work of Nobles (230) on the *Trametes serialis* complex. The work of Cabral (59*a*), however, indicates that the method has its limitations.

ESTABLISHMENT OF HEART ROTS

Much more is known concerning the chief places of entry of heart-rot fungi into trees than of the details of inception of the resulting decay. First in importance among places of entry are wounds from various causes: (*a*) fire; (*b*) conditions associated with weather, including breakage from wind, ice and snow, wounding from falling trees, wounding and shattering from lightning, cracks from freezing, and sunscald and winter injury of bark; (*c*) activities of man in logging, pruning, cultural operations, blazing land lines or trails, blasting and construction, the striking of trees with moving vehicles, and the misuse of axes and knives; (*d*) gnawing, trampling or rubbing by animals; and (*e*) mining of the cambium by insects.

In North America (217) and parts of Asia, fire unquestionably

has exceeded all other causes of wounds through which decay fungi enter. Hedgcock (138) reported indications that over 90 per cent of the cases of basal rots in hardwood forests of the eastern United States entered through wounds from fire, Kaufert (173) estimated that more than 90 per cent of the total decay in bottomland hardwoods of Louisiana was of that origin, and 97 per cent of the wounds found by Hepting and Hedgcock (149) in the principal Appalachian hardwood species were from fire, to which 70 per cent of the cull in the trees was chargeable. Wounding from fire is almost equally important as a source of decay in the coniferous forests of part of the western United States (295).

Considering shade and orchard trees as well as forest trees, wounding by man probably ranks next to fire in providing places of entrance for decay fungi. Wounding is an almost invariable accompaniment of logging in many parts of the world, and in the United States it has been increasing in amount with the wider adoption of selective methods of cutting and of the use of tractors in the woods. Heart-rot fungi become established freely in wounds of this type in tree species with non-resinous woods such as the true firs and western hemlock (100, 257, 336, 343), and even in some species with resin ducts in the wood, as spruce (136, 343). In shade trees, including those along roadsides and streets, man-made wounds from pruning, construction and the careless operation of vehicles are probably almost as important, if not equally so, from the standpoint of decay, as those resulting from ice and wind breakage. Pruning wounds also are a major source of entrance for heart-rot fungi in orchard trees (97) and may be important in forests (271, 303). In many parts of India the practice of lopping branches of forest and shade trees for fuel and fodder and for bedding material for cattle is widespread. The resulting rough wounds provide very favorable entrance courts for heart-rot fungi (13, 179).

A special class of wounding by man arises in the removal of companion sprouts during thinnings in sprout oak stands. When sprouts two inches or more in diameter are removed, heartwood is exposed and wounds are created that are slow to heal, offering very favorable opportunities for the start of decay (274). Likewise in conifers, stumps left from the removal of one member of double stems during thinning operations may permit the entry of butt rots

such as *Fomes annosus* and *Armillaria mellea.* Closely allied with these are the residual wounds from stumps in cut-over oak forests that have regenerated through stump sprouts. If these sprouts arise above ground level they are very likely to form a heartwood connection with the decaying stump after 10 to 15 years, permitting the decay to progress into the base of the sprout. On the other hand, if the origin is at or below ground level, a connection through which decay may enter is much less likely to develop, and such sprouts remain relatively free of basal rots (273, 275).

Even quite small man-made wounds, such as the holes left by the extraction of increment cores, may provide entrance points for heart rots when they penetrate deeply (152, 203). Although disinfection of the increment borer between extractions was found to have no noticeable effect on the amount of resulting decay and stain in two areas where tested (152), it is possible that indiscriminate boring of trees in stands with considerable established decay might serve to transplant the decay fungi to uninfected trees.

Breakage of tops and branches from accumulated ice or snow is widespread in all the cooler forested regions of the world, and the wounds thus caused directly expose heartwood and are often jagged, providing particularly favorable sites for the establishment of heart-rotting fungi (189, 270). Wounds from falling trees not associated with logging provide entry for fungi causing an appreciable part of the decay in virgin stands of some western North American conifers, particularly western hemlock (99). Winds undoubtedly are primarily responsible for most of this injury. Other wounds, arising from adverse weather conditions and from injury by animals and miscellaneous causes, are less often entry points for fungi, but some decay is traceable to all of them.

Branch stubs and open knots were early recognized as entrance courts for heart-rot fungi, particularly for *Fomes* (*Trametes*) *pini,* undoubtedly the most widespread and important single decay organism in conifers in the world (171). Hartig's conclusion in 1874 (134) that this fungus enters almost exclusively through branch stubs has been confirmed by many other investigators, both in Europe (196, 197, 221) and America. In the United States and Canada specific information on this point has been obtained for Douglas-fir (42), Sitka spruce (32) and western hemlock (99) on the Pacific Coast, for loblolly and shortleaf pines in Arkansas and

Texas (146), for western white pine in Idaho (324), and for eastern white pine in Ontario (133). Studies have shown that branch stubs and knots play the same role for *Stereum sanguinolentum* in balsam fir in eastern North America (175, 207, 301, 303) and for *Echinodontium tinctorium* in western hemlock in Idaho (323), resulting in very prevalent trunk rots in these respective species. In addition, evidence is accumulating that *E. tinctorium* characteristically enters true firs in the western United States by these same avenues instead of primarily through fire wounds as was formerly believed. For hardwoods less information is available on the role of branch stubs and knots as entrance courts for decay fungi than for the conifers, but considerable decay is traceable to them (88, 91, 148), and in species such as aspen they may be the chief places of entry of heart-rot fungi (285).

A few fungi, of which *Polyporus anceps* (*P. ellisianus*), the cause of western red rot in ponderosa pine, is perhaps the best example, rarely enter through knots or stubs of shed branches, but must first establish themselves as saprophytes in bark-covered dead branches (202), from which they slowly progress through the branch base to the heartwood of the tree. Andrews and Gill (5, 6) found that *P. anceps* seldom becomes established in branches under one inch in diameter and that, accordingly, nearly all entrance of the fungus takes place from dead branches over this size.

A number of fungi that typically produce basal rots in trees are able to enter through roots as well as through basal wounds. Important species in this group are *Polyporus schweinitzii, P. balsameus, P. circinatus, Fomes annosus, Corticium galactinum, Poria cocos, P. weirii, Ganoderma pseudoferreum* and *Armillaria mellea.* Most of them are known to be pathogenic at least under some conditions (37, 82, 120, 129, 157, 224, 258, 259, 262, 309, 319, 328) and are able to enter and kill roots progressively until they reach the heartwood at the base of the tree. Some, such as *Fomes annosus* on a number of hosts under favoring site conditions, characteristically enter roots through tissues killed or diseased from other causes (157), but once established are able to extend pathogenically into live portions of the root (262). However, *Fomes annosus* may also enter uninjured roots directly as a complete pathogen (261, 319). Others probably reach the heartwood only through roots that are already dead from girdling, drought, lack of sufficient oxy-

gen or other unfavorable conditions, and progress into the basal heartwood without any true pathogenic killing of host tissues. Field indications suggest that *Polyporus schweinitzii,* when it enters through the roots, usually falls in this class (147), although the direct pathogenic invasion of white pine seedlings by the fungus has been demonstrated (321), and it has caused serious damage in individual young white pine (338) and Douglas-fir (139) plantations on the Atlantic Coast. Another butt-rotting fungus that is reported to enter often through dead roots is *Poria subacida* (175, 207, 238). Gosselin (129) obtained presumptive evidence that *Polyporus circinatus* first establishes itself in a normal mycorrhizal relationship on the roots of spruce in Quebec and later invades the lateral roots as a pathogen, extending then into the butt of the tree as a heart rot, but there is some inclination on the part of other workers to doubt this.

Cankers, galls and swellings produced by fungi and mistletoes comprise still another class of entrance courts for heart-rot fungi, after these malformations have reached sufficient age for the development of necrotic tissues (127). In western hemlock, Englerth (99) found that 31 per cent of the decay in the stands sampled was traceable to mistletoe cankers and swellings, and Gäumann (122) points out that the principal significance of stem cankers from the rust, *Melampsorella caryophyllacearum,* on firs in central Europe is their role in serving as entrance points for the heart-rotting fungi, *Polyporus* (*Fomes*) *hartigii* and *Agaricus* (*Pholiota*) *adiposus.* Decay likewise sometimes becomes established in hardwoods through fungus cankers (27, 61, 216). Conversely, a few decay fungi, following development in the heartwood, are themselves producers of cankers through their ability locally to kill sapwood (61, 65, 66, 90, 91, 236, 271, 297).

Not all of these possible places of entrance are wholly without protection against fungus invasion. As pointed out by Liese (196), a tree does not play a passive role during the death of one of its twigs or branches. Protective substances in the form of resins, gums and other infiltration products are laid down in the branch base (213, 288, 305), not only as a protection against the entry of harmful organisms from the outside, but also to prevent loss of water and maintain normal hydrostatic pressures within the tree. Wounds in the sapwood of species of conifers with resin ducts nor-

mally present there are quickly sealed by the resin liberated as a wound reaction (158). In a number of hardwoods a similar protective barrier is formed by deposition of gums and phlobaphenes (123, 145, 249, 305). Even where heartwood is exposed in wounds from repeated fires in large conifers, the wood back of the wound is often quite heavily resin infiltrated, especially in the pines.

These deposited barriers are not effective against all fungi and frequently they do not remain intact indefinitely but are ruptured by checks resulting from drying out of the exposed wood or by galleries created by wood-boring insects, allowing a passageway through the barrier zone for fungus spores or mycelium.

Whatever the avenue of entrance, the common means of initiation of decay, according to accepted views, is through the germination of spores of a suitable fungus after their deposition in contact with non-living wood that the fungus is capable of attacking and entering. Exceptions are those cases in which the fungus is merely extending from an already established body of decay, as from stump to stump sprout through a heartwood connection or from a decayed to a sound root by means of rhizomorphs or live mycelium.

Basidiospores of most heart-rotting organisms germinate readily in the laboratory on agar medium or in water; but some fail to germinate, or germinate with difficulty, and in some, germination is delayed. Bailey (16) was able to obtain germination of basidiospores of *Polyporus rheades* only in a malt extract medium in which mycelium of the fungus had been growing, and of *Polyporus basilaris* (15) only when a few shavings of wood of *Cupressus macrocarpa* were added to peptone-glucose agar. From a comprehensive investigation of basidiospore germination in the Hymenomycetes, including many heart-rotting species, Kneebone (184) concluded that no single factor is limiting in cases of non-germinability. Various reported methods for stimulating germination, including activation by yeasts (Fries (114)), were tried without promising results. However, low temperature treatments were effective for a number of species.

Germination in nature at usual places of entry has not been closely followed, but Haddow (133) observed that the basidiospores of *Fomes pini* are exceedingly delicate when freshly cast and that only a short period of drying destroys them after they have begun to germinate. In a dry state, however, the spores of some Hymeno-

mycetes retain their viability quite well, as demonstrated by Meyer (219) who found that 25 per cent of the basidiospores of *Fomes fomentarius* still retained their germinative capacity after dry storage in a test tube in the laboratory for one year.

In the open the chances for establishment of a wood-destroying fungus from spores is undoubtedly increased by protection against dislodgment and drying out, such as that offered by seasoning checks or other small openings into the wood. Thus Lagerberg (189) found that the establishment of decay following snowbreak in spruce tops had been favored where tongues and splinters had been pulled out of the wood at the break. Formerly it was believed that most heart-rotting fungi could enter a tree only through exposed heartwood (217, 221), but in Ontario, Haddow (133) found that *Fomes pini* had entered the bases of white pines through stubs of twigs and branches that were as little as one-twentieth inch (1.3 mm.) in diameter and that had been alive only five or six years. Not only would formation of natural heartwood in twigs of this size and age be inconceivable, but they had died long before heartwood had been formed in the main trunk. Accordingly, it appears that the earlier ideas, while no doubt correct in the main, must be modified in some degree to allow for cases such as those found by Haddow. The latter author believes that basal infections of *Fomes pini* observed elsewhere and ascribed to entry through the roots by Runnebaum (276), Singh (296) and others, probably entered in fact through such small basal branch stubs. However, Bagchee and Bakshi (13) report that Childs and Clark in the United States have proved quite conclusively that this fungus occasionally spreads through root grafts, though they regard spread by this means as of no practical importance in the Douglas-fir forests of the Pacific Northwest. Liese (196) concedes that *Fomes pini* is capable of establishing itself in exposed sapwood, but states that, because of its slow growth, other, more rapidly growing decay fungi are almost certain to overwhelm it before it can reach the normal heartwood. Ability to enter the heartwood through wounds may thus depend in part on the relative rate of progress of a particular fungus through dead sapwood. It should be remembered in this connection that in many species sapwood exposed by wounding is rather rapidly transformed through traumatic response into pathological heartwood (59), unless the wound is quite large, and that

such wound heartwood compares in all apparent respects with normal heartwood (188).

Infections by any particular heart-rotting fungus in a tree may be either single or multiple. By testing isolates of *Fomes pini* from the heartwood of individual Douglas-firs for compatibility in culture on agar media, Roth (*275a*) concluded that the decay in 70 per cent of the trees arose from single infections; in 25 per cent it represented two infections; and in 5 per cent, more than two infections. Incompatibility of isolates was the criterion used for separating infections.

NATURE OF THE DECAY PROCESS

The foundation of our modern understanding of the decay process in trees was laid some 70 years ago by the perception of Robert Hartig (134, 135) that decay is the result of the action on wood of specific associated fungi and that these must enter the tree from the outside before decay can be initiated. Prior to that time the interpretation of the decay phenomenon had been clouded by the then current belief in spontaneous generation. Hartig also perceived that the process is chemical in nature, resulting in the loss of constituents of the cell walls. However, it was not until a number of years later that the means by which the fungi accomplish the degradation of wood tissue was made clearer by the demonstration that they secrete diffusible enzymes capable of acting on specific chemical constituents of wood (40, 87). An individual fungus ordinarily produces a number of these, from 12 to 21 having been determined for various heart-rotting species (39, 119, 283, 284, 286, 341). Since the function of most of the enzymes is to convert the wood substance into food materials available to the fungus, it could be anticipated that they would be largely extracellular in concentration (76), and this has been shown to be the case (39). An exception is catalase which acts principally in fungus respiration and thus functions intracellularly. Among the enzymes chiefly extracellular in action are those capable of decomposing polysaccharides and lignin, but small amounts of lipolytic and proteolytic enzymes are present also (76).

Basically, from the chemical standpoint, decay is typically a hydrolysis through which the substance of the cell wall is converted into gums, soluble pseudogums and finally into sugars which consti-

tute the source of carbon for the nutrition of the attacking fungus (76, 206). However, between individual species of fungi there is a wide variation in the order and proportion in which the major wood components are attacked, resulting in different characteristics of the rot produced (70).

The decay process ensues after initial penetration of the wood by fungus hyphae. It was formerly believed that this penetration was at least in part by mechanical force exerted by the growing hyphal tip, although in Sitka spruce Cartwright (72) had noted partial dissolution of the cell wall where hyphal tips of *Poria monticola* (*Trametes serialis*) came in contact with it. In a careful study of this question, Proctor (247) demonstrated that dissolution of the cell walls by enzymatic action took place ahead of the hyphal tips, resulting in holes, usually termed bore holes, in the walls through which the hyphae pass. He was unable to find any evidence of mechanical penetration at any time.

STAGES OF DECAY

For most heart-rotting fungi, initial penetration of the hyphae into sound wood is made without any immediate change in the macroscopic appearance of the invaded wood. This initial or invasion phase of the decay process has sometimes been termed the invisible or hidden stage (298). Determinations of the width of the zone through which penetration has occurred in advance of any visible discoloration or change in wood texture have been made both by microscopic examination for the presence of hyphae and by cultural means (21, 41, 160: p. 80, 178, 325). Some of the most comprehensive investigations have been those reported by Roth and Sleeth (275) for common butt rots in oaks. Cultures were made from samples taken at one-foot intervals beyond visible evidences of decay. The maximum penetration found beyond visible discoloration was 72 inches (183 cm.) reached by *Polyporus sulphureus*. The combined data from all sources indicate that penetration is much greater in a vertical than in a horizontal direction, that with some fungi the distance may be so short as to be almost negligible, but that with a number of heart-rotting fungi an average extension of one to two feet (30–60 cm.) beyond the last visible signs of decay may be anticipated.

The stages of decay most commonly recognized are the incipient

or early stage and the advanced or typical stage (298). An intermediate stage is sometimes distinguished. In the incipient stage, the wood has become discolored to at least some degree but shows little evidence of a change in texture, although its physical characteristics may no longer be equal to that of sound wood. In the advanced stage, decomposition of the wood has taken place to a degree in which the appearance, character and specific gravity have been definitely altered and the condition has been reached that we ordinarily refer to as rot or decay (159, 160). It is in this stage that the characteristics of the different decays, as determined by the activities of the enzymes produced by the respective causal fungi, become apparent, resulting in different types of rot. A fourth stage, termed the final stage, in which destruction of the wood substance has progressed very far, is sometimes differentiated.

The relative extent of decay in the incipient stage varies widely for different causal fungi and different kinds of wood attacked, from a few inches to many feet in lineal extent. It is usually least in decays of the brown friable type.

By the time the advanced stage is reached, the initial hyphae of the responsible fungus often disappear, leaving only the hyphal holes through the degraded cell walls to mark their former location (159: p. 549). However, as long as the decay process continues, the causal fungus can usually be recovered, even from wood in the advanced stage of decay.

TYPES OF HEART-ROT DECAY

For convenience in differentiating between decays, several classifications have come into use, based on the color or character of the decay or the part of the tree affected (159). They are not sharply defined and intergradations occur, so they can not be considered as absolute, even though very useful.

On the basis of the predominating type of decomposition, most decays group either into white rots, in which all chief constituents of the wood are attacked, or into brown rots, in which celluloses are removed, termed, respectively, corrosion-type and destruction-type rots by Falck and Haag (106) from the standpoint of the nature of the chemical degradation processes involved. Björkman et al. (36) further differentiate the broad corrosion-type rots into corrosion rots proper and white rots. Utilizing the fact that decay

fungi causing typical white rots secrete an oxidizing enzyme or oxidase, while those inducing brown rots do not, Bavendamm (20) developed a laboratory method for distinguishing fungi of the two groups in culture, based on the presence or absence of an oxidase reaction. A test of this reaction by use of a guiacum solution was later announced by Cartwright and Findley (76), and, more recently, a method utilizing the dye gentian violet has been reported by Preston and McLennan (245). Over 200 wood-decay fungi have been tested by the Bavendamm method for the oxidase reaction by Davidson and co-workers (89) who found that 96 per cent of those associated with white rots showed a positive reaction, and 80 per cent of those associated with brown, friable rots gave no reaction.

Good examples of white rots are those caused by *Stereum gausapatum, Poria andersonii, P. obliqua, Polyporus glomeratus* and *Fomes igniarius* in hardwoods, and *Poria subacida, Polyporus anceps* and *P. borealis* in softwoods.

The brown friable rots are not so numerous in hardwoods as white rots, but there are a few important ones, such as that from *Polyporus sulphureus.* In softwoods they are quite numerous. The decays from *Polyporus schweinitzii, P. balsameus, Coniophora cerebella* and *Fomes pinicola* are good examples. Most brown friable rots occur as solid columns, often occupying practically the entire cross section of the heartwood in the infected portion of the trunk or branch; but in a few, such as those from *Polyporus amarus* and *Poria sequoiae,* the decay develops in irregular pockets in the heartwood. Decay fungi causing brown rots are not able to destroy more than 65–70 per cent of the wood substance, leaving a lignin or lignin-like residue resistant to decomposition, while many white-rot fungi are able to destroy wood almost completely (109).

White rots may be further divided into pocket rots, white stringy rots, yellow or yellowish brown stringy rots, and others, depending on appearance and texture. Brown rots may also be further divided into light brown or reddish brown groups or into those with large or small pockets.

None of these classifications aids greatly in the determination of decays attributable to specific fungi except within local areas, or more generally for a few cases of white pocket rots. The decay

from *Fomes pini* usually can be identified by the appearance of the rot, except in incipient stages or in hosts in which the features differ from the usual for this fungus. That caused by *Stereum subpileatum* may be identified from the honeycomb pattern of the lens-shaped pockets and the musty odor of old honeycomb produced when the decay is in active condition (200). The decay of *Polyporus berkeleyi* can also usually be identified from its characteristic strong anise-like odor, in combination with its stringy type and the location in the butts of hardwoods (199). *Lentinus lepideus* is another fungus for which the characteristic fungus-oleoresinous odor of the decay aids in its identification (318), but *Polyporus schweinitzii,* which causes a brown butt rot in numerous coniferous hosts, apparently sometimes induces a distinctive aromatic odor when active in decay, and sometimes results in no odor (324).

Identification of individual rots according to causal fungi is made much more accurately through isolation and study of the fungi present in the affected wood than by judging from general habit or appearance. They often can be induced to fruit in culture, and sporophores obtained in that way, even though abortive, frequently are valuable aids in identification (223).

To be most effective, the study of isolates should have as a foundation a reference collection of cultures isolated from identified sporophores of heart-rotting fungi (91), a foundation requiring much time and effort to acquire and maintain. A good reference collection not only aids in more accurate classification of species of fungi associated with undetermined decays (63, 64, 68, 230), especially in groups such as *Poria* where identification of sporophores is difficult; it also permits exchange of cultures between workers, even at great distances, and makes possible more detailed comparisons of strains of fungi for varietal differences. Thus it has possibilities of greatly reducing confusion in nomenclature (230). In the absence of a reference collection, cultural keys such as those by Fritz (115), Campbell (60, 91), Baxter (24), Nobles (231), Refshauge and Proctor (250) and Robak (266) are very useful.

The microscopic characteristics of hyphae are a material aid in the identification of wood-rotting fungi, both when diagnosis is attempted from the decay (77, 159, 314) and when based on cultures (89). These include the presence or absence of constrictions and the type of constriction in passing through cell walls, the pres-

ence or absence of clamp connections, the production of setae, vesicles or other special structures, the formation of incrustations, and other features. Up to the present, these microscopic characteristics of hyphae have been used only for their contributary value in identification, but Proctor (247) has expressed his confidence in the feasibility of employing their features in decayed wood as a primary basis for determining the fungi involved.

PROGRESS OF HEART ROT FUNGI IN TREES

The rate at which decays may be expected to extend into the sound heartwood of trees or increase in forest stands is often an important consideration in forest management. It must be taken into account in setting up the basic logging plan for forest properties in order to hold losses of wood volume from decay to a minimum, and in many cases it must be weighed by the tree marker in deciding which trees to cut and which to leave for the next cutting cycle on a particular forest tract.

Three methods have been employed for obtaining information on the progress of decays. The one yielding the most precise information consists of inserting into sound trees, under aseptic conditions, pure cultures of the particular heart-rotting fungus under test, plugging the insertion holes, and cutting the tree at a later time to determine the spread of the decay during the intervening period. The second method takes advantage of naturally established cases of decay in which the year or period of entrance can be approximated. The extent from the place of entrance is measured in felled trees as in the first method. In the third method, sample trees representing different age classes of a selected tree species are felled and dissected, and the extent of all decay present is measured, regardless of opportunities for determining the probable time of entrance of the causal fungi. The first two methods are used for determining the progress of decay in individual trees, while by the third method a measure of the general increase in decay with age in timber stands is obtained.

PROGRESS OF DECAY IN INDIVIDUAL TREES. Results of tests by the first method, employing artificial inoculation, have been too few to give any comprehensive measure of the average rate of extension of heart rots, but they have been valuable in demonstrating the wide differences in the rate of progress of decays between trees

from as nearly uniform beginnings as possible. In four trees of *Pinus sylvestris* artificially infected with *Fomes pini* and opened 7¼ years later, Möller (222) found that decay had progressed upward a minimum distance of one meter and a maximum of two meters or average annual progress of approximately 14 and 28 cm. (5.5 and 11.0 in.), respectively. Still greater differences were shown in red beech, a species possessing ripewood instead of true heartwood, infected with various decay fungi by Münch (226). After 3½ years, *Fomes fomentarius,* an important beech decay fungus, had extended in one tree for about 30 cm., with early typical decay apparent in only the first 10–15 cm. In another tree, a suppressed one, the mycelium of the fungus had extended for more than one meter, with an intensive white rot for half that distance. *Stereum purpureum,* for which a maximum extent after 3¾ years of 2.1 meters was measured, showed differences of about the same proportion. Following the inoculation of one tree each of seven species with *Fomes pinicola* in New York State, Hirt and Eliason (156) obtained a maximum extension from the place of inoculation of over 56 inches (1.1 m.) in *Picea rubens* after ten years, but only 13 inches (33 cm.) in *Tsuga canadensis.* More recently, Rennerfelt (254) has inoculated 18 spruces with *Fomes annosus* through increment bore holes and obtained a maximum spread up the heartwood of 216 cm. (85 in.) in 25 months. Average progress was much slower: 26.1 cm. upward and 31.7 cm. downward, or a total extent of 57.8 cm. (22.7 in.) per year.

One general criticism that can be made of most, if not all, of the artificial-inoculation experiments that have been undertaken so far is that they have not duplicated the manner or conditions of infection as they occur in nature, particularly in the matter of aeration or of opportunities for contamination by other organisms. There is, in consequence, some question of how good an index the results provide of the rates of advance of decays that may be expected in nature.

Very much wider differences in rate of progress have been found in decays resulting from natural infections for which the year or period of origin could be approximated. Thus in oak in Germany, Münch (227) found that average annual spread of *Fomes igniarius* in one direction in the heartwood had varied from 1.9 to 25 cm. In Sweden, Lagerberg (189) measured the progress of rots following

snowbreak in the tops of spruce and obtained annual rates of from 0.5 to 112.5 cm. from breaks four to five years old. Haufe (136), in Saxony, found one instance in which decay in spruce had extended upward from a basal logging wound to a distance of ten meters in 19 years, or more than 52 cm. per year. For *Polyporus amarus* in California incense-cedar, Boyce (41) found rates for total extent in the heartwood that varied from .002–.003 ft. (0.6–1.1 mm.) to 0.53–3.09 ft. (16–94 cm.) per year. In black oak in the Mississippi delta, Hepting (142) found that in one-sixth of the cases measured the average annual upward extension of decay from basal scars was less than .02 ft. (0.6 cm.), and in one-sixth it was over .28 ft. (8.5 cm.), while for ash the values for the sextile limits were .04 ft. (1.2 cm.) and .31 ft. (9.4 cm.), respectively. Actually, such differences may be more apparent than real, unless care is taken, when observations are made, to determine in each case that the decay fungus concerned is still in an active condition. Based on the results of multiple culturing from butt decays in sprout oak stands in the eastern United States, Roth and Sleeth (275) concluded that a significant proportion of the third of decay cases from which no decay fungus was obtained must have been inactive and thus no longer progressing in the heartwood. There is reason to believe that the dying-out of heart-rotting fungi after establishment and initial progress in living trees is not uncommon, and inclusion of such cases, after death of the causal fungus has occurred, in determining the rate of progress of decays gives a somewhat false picture of the variation in rate that can be anticipated, even though the information is useful in determining the general relation of decay to timber stands. Recent observations by Rishbeth (262) on species succession in butt-rotted conifers suggests that this may constitute another source for variability in decay rates that may be of greater importance than now realized.

Differences in the rate of progress of decay not only appear in different trees of a species and between different host tree species or different heart-rotting fungi, but they may appear between different infections by the same fungus species in different parts of the heartwood of a single tree or as a result of initiation at different seasons of the year. Differences within individual trees are to be anticipated, especially in large trees, by differences in rate of growth during the life of the tree and consequent differences in the

structure of the wood produced, by differences in the kind and concentration of extractives and possibly in the content and composition of gases These will be discussed in a later section. Where decays are initiated through wounds in the sapwood or enter trees characterized by ripewood instead of true heartwood, the growth activities of the tree, as these influence its defense reactions, are likely to result in differences in the initial spread of the decay fungus (305). An indication of the effect of these differences in sapwood was obtained by Münch (226) from inoculations with *Stereum purpureum* into two young balsam poplars as nearly comparable as possible. From an October infection, when the tree was entering its dormant period, the fungus had penetrated from 20–30 cm. in both directions by late that fall, while from a corresponding inoculation made in the companion tree the following June, during the height of the growing season, the fungus had progressed less than ten cm. by August.

In determining the rate of progress of decay from a known time and place of initiation, the length of time elapsing before measurements are made is evidently of some importance.. The observations of Hepting (143), Münch (226, 227), Lagerberg (189), Zöhrer (343) and others indicate that the initial rate of extension of a heart-rot fungus in a tree may be much more rapid than that prevailing later, and some fungi may stop growth almost completely after a relatively rapid initial advance. Accordingly, measurements taken too soon after initiation of decay may give an erroneous impression of the sustained rate of progress to be anticipated over a longer period. Moreover, decay rates calculated from entry points such as trunk wounds or broken tops may differ greatly, depending on the particular fungi that become established. Below broken tops from glaze damage in black cherry and maple, Campbell and Davidson (67) found that the decay fungi present were almost entirely sapwood-rotting organisms, chiefly *Polyporus versicolor* and *Stereum rameale*. Forty months after the breakage had occurred the rate of advance of the decays was slowing materially, and the authors anticipated that, as the entry wounds healed, the decay fungi would eventually die out.

For application to timber stands the average rate of extension of decay columns is of much more practical value than the rate for individual cases (142), although it is to the latter that we must

look for a basic understanding of the reasons for the differences that affect the average. In general, the tendency among foresters appears to be to over-estimate probable rates of decay in planning the cutting of defective stands (46: p. 346). The investigative evidence so far available indicates that the rate is relatively slow in most tree species. For *Fomes pini* in *Pinus sylvestris* in Germany, an average total extension of 20–25 cm. (8–10 in.) per year in trees with less resinous heartwood, and 8–15 cm. (3–6 in.) in those with a higher resin content is indicated (196). For decays entering fire wounds in the Mississippi delta, the average annual progress was found to be 2.3 in. (5.8 cm.) in black oak, and 1.5 in. (3.8 cm.) in ash (142), while in oaks of sprout origin without fire wounds in the eastern United States, the average yearly rate of advance varied from 2.0 to 3.0 in. (5.1–7.6 cm.) for *Stereum gausapatum* in different oak species (275). Since the decays in oaks and ash on which these rates were based originated in almost every instance at the base of the affected trees, they represent advance in an upward direction only, while the extension for *Fomes pini,* which ordinarily enters through branch stubs, represents progress both upward and downward from the place of origin. Thus, in considering the rate of decay with respect to its effect on merchantable volume, it is necessary to differentiate between decay fungi entering at the base of a tree or in a broken top, where they can progress in the trunk in only one direction, and those entering at intermediate locations where they have the opportunity to advance in both directions. It follows that, with the same potential rate of advance, butt and top rot fungi can be expected to make less total linear progress in a given time in the trunks of affected trees than fungi ordinarily entering trunks through knots, branch stubs or branches. The importance of this consideration for an understanding of the progress of cull in balsam fir in New England is pointed out by Spaulding and Hansbrough (301). *Stereum sanguinolentum,* causing the principal trunk rot in this tree species, not only spreads more rapidly in one direction than the butt rots that occur in it, but it also grows both upward and downward from the place of establishment, while the butt rots can progress only upward. Thus, though butt rot infections become established sooner and in greater numbers than trunk rots, the volume of cull from the latter soon outstrips that for butt rots.

Other reports on average annual rates of progress of decays in conifers are of 15.9 cm. (6.2 in.) and 18.3 cm. (7.2 in.) in one direction from blaze wounds in spruce in Sweden (98, 103), and 19.2 cm. (7.5 in.) in both directions from wounds in spruce in the German Alps (343).

PROGRESS OF DECAY IN STANDS. Studies to determine the progress of decay in individual tree species or in timber stands have been concentrated largely in the United States and Canada. This has been partly because of proximity to the pioneer work of Meinecke (214) in southwestern Oregon, which stimulated similar studies on other areas (207), and partly to the special applicability of such studies to defective virgin stands of timber, such as are still found in parts of western North America. Moreover, virgin stands provide very suitable material for studies of this kind because of the wide range in the age classes of trees that are ordinarily represented in them.

Most of these investigations have been primarily to develop facts and relationships for application in forest management and, accordingly, have been more concerned with the commercial aspects of decay as they affect utilization than with determination of the specific progress of decay itself in timber stands. Consequently, many of the results have been expressed as cull resulting from decay rather than as net decay volume. As pointed out by Kaufert (175), cull is likely to vary according to the character or intensity of prevailing or anticipated utilization, and cull volumes thus depend on the particular culling standards employed. An illustration of the effect that different culling standards may have on cull percentages derived from the same basic material is provided by the investigation by Bier, Salisbury and Waldie (33) of cull from decay in *Abies lasiocarpa* and *A. amabilis* along the upper Fraser River in British Columbia. With pulpwood as the anticipated form of utilization, cull, under what the authors termed the "western basis" in cubic feet, which closely approximated actual decay volume, was found to range from 6.7 per cent in trees 80 years of age to 34.7 per cent at 210 years. Under the "eastern basis", which the authors regarded as closely approximating actual pulpwood utilization standards in other regions, the same basic data gave cull per cents ranging from 10 per cent at 80 years of age to 77.4 per cent at 210 years, or more than double that obtained by the "western

basis" for the upper age classes. Cull per cents obtained by application of standard scaling rules to trees of saw-timber size from the same basic sample, but figured in board feet instead of cubic feet, proved to be intermediate in values, ranging from 14.7 per cent at 100 years to 42.5 per cent at 210 years. Fortunately, a number of the investigators in this field have compiled their data on the basis of actual volumes of decay as well as on a cull basis.

From a survey of available reports of investigations, it is apparent that for particular species in favored locations, timber may remain extraordinarily sound to advanced ages. Probably the soundest yet reported for its age is Sitka spruce in the Queen Charlotte Islands of British Columbia, in which decay was found to amount to only 0.7 per cent of the merchantable volume at 200 years, and only 26.6 per cent at 750 years of age (32). Maximum decay increment amounted to only 0.06 per cent per year, reached in the oldest trees between the ages of 700 and 750 years. In contrast to this extremely slow rate of decay progress in Sitka spruce is that for aspen in the Lake States, in which total rot, including the incipient stage, was found to have already reached 8.1 per cent of total tree volume at 20 years and 33.8 per cent at 80 years (285). Maximum annual increase occurred between the ages of 30 and 40 years, and amounted to 0.49 per cent per year. For most of our more important timber species in which decay from heart rots is a major consideration, the rate of progress falls in an intermediate range between the extremes cited (46: p. 346).

The figures that have been presented are averages representing a number of samples of the host species within the particular region concerned, and thus the rates of progress shown also represent averages. In many species, individual stands occur in which progress of decay is very much faster than the average rate. An example of the variation in defectiveness that may be found within even a relatively limited area is provided by a study by Englerth (99) of decay in western hemlock in western Oregon and Washington. On one plot, on which the hemlocks averaged 214 years of age, decay amounted to 61.1 per cent of board foot volume, while on another only four miles distant, with hemlocks averaging 180 years, only 14.2 per cent of decay was found. Average decay percentages based on all sample plots were not reported in this study, but an inspection of the data indicates that for the respective ages

the per cent of decay on the first plot was far above average and was slightly below average on the second. Still greater differences were found by Boyce (45) between more widely distributed plots in Douglas-fir in the same region. The trees on two of these plots were of equal average age, 245 years, but only 0.1 per cent rot was present on one and 16.9 per cent on the other. The average at this age for Site II plots was approximately 7 per cent, so the rate of progress on the second plot had evidently been more than twice that of the average, while on the first plot it had been negligible. It follows that, in arriving at conclusions concerning the progress of decay for any particular timber stand, adjustments must be made to allow for the decay prevalence there as compared with that for the reference standard, such as the averaged results of a decay study, on which the conclusions are to be based.

Differences in the progress of decay within a species may sometimes be occasioned by differences in the species of causal fungi, each with its own particular rate of development. For many years forest pathologists assumed, on the basis of the study by Weir and Hubert (323) in northern Idaho, that the fungus *Echinodontium tinctorium* was the chief species concerned in heart rot of western hemlock in the Pacific Northwest. However, Englerth (99), in his study recently referred to, found that this fungus is rarely present in the commercial stands of western hemlock in western Oregon and Washington, and that the chief decays there are from the butt-rotting fungus *Fomes annosus* and the trunk-rot organism *Fomes pini.* Recently, within a much more limited area in the Big Bend region of British Columbia, Foster and Craig (111) have found different decay fungi predominant in this tree species on areas only 30 miles apart in the same river valley. Decay from *Echinodontium tinctorium* was strongly predominant on one area, while that from *Fomes pini* contributed the major volume on the other. Although specific information on comparative rates of progress of these species in the heartwood of western hemlock is lacking, it is highly improbable that the rates would prove to be equal.

Determinations of the decay present at different ages in the life of species or stands from which figures on the progress of decay have been derived have all been made on trees currently present in the stands and do not reflect the influence of decay removal through mortality of affected trees. If mortality were evenly distributed

over different age groups of trees without reference to their defectiveness, the losses would have no influence on comparative decay volumes at different ages and could be disregarded. For a number of species, however, it is known that decays are precursors of mortality through the weakening of bases or trunks so that the affected trees become subject to breakage or windthrow. In balsam fir, windthrow from butt rot is prevalent after the age of 70–80 years (175, 207, 301). It is also common in white spruce affected by butt rot from *Polyporus circinatus* (82, 129). For western hemlock, Englerth (99) states that there is a continual dropping out of trees from breakage or windthrow occasioned by decay from about 100 years on, and that "at about 300 years decay becomes so extensive in many of them that they become easy victims to windstorms".

In Douglas-fir, Boyce (45) points out that when an old stand is breaking up, the percentage of decay in the survivors may decrease through the dropping out of decadent individuals. Recent investigations on this species (46*a*) show that there is a cyclic fluctuation in decay volume as stands increase in age, attributed to the dropping out of defective trees. The stand ages at which the maxima, two in number, occur were found to vary according to site quality. In the late stages of stand break-up, the normally predominant decay from *Fomes pini* may be supplanted in importance on a total volume basis by that from *Fomes laricis* (*F. officinalis*) (320). In their study of Sitka spruce in the Queen Charlotte Islands, Bier, Foster and Salisbury (32) point out that relatively low decay volumes in the upper age classes do not present a true picture of the progress of the decay in stands, since the trees composing these classes are residuals, as indicated by the abundance of associated snags and down trees, windthrown and broken as a result of decay.

Obviously, the progressive removal, through mortality, of badly decayed individuals from a stand would tend to reduce the percentage of decay as represented by the remaining trees. It follows that rates of progress of decay in stands, derived from percentages of decay present in the living trees, will not reflect the true progress of decay beyond the age at which the selective loss of badly decayed individuals begins to occur, and that the true rates of progress beyond this age will be higher than the derived rates.

CONDITIONS INFLUENCING PROGRESS OF DECAY IN INDIVIDUAL TREES

Considering its basic significance, our knowledge of the conditions that favor or restrict the growth of heartwood-destroying fungi in trees is surprisingly incomplete (345). Where particular aspects of the physiology of these fungi have been investigated in the laboratory, the intermediate steps by which the results could be translated into conditions actually occurring within the living tree have not always been carried out. In consequence, there are many gaps in our information on the subject.

EFFECT OF GASES. Observations by field workers on heart rots have long suggested that the amounts and composition of gases present within heartwood may exert a marked influence on the progress of decay organisms. This view was supported by the early conclusion of Münch (225, 226) that oxygen supply is a chief factor in regulating fungus development within the wood of trees, but the later investigations of Bavendamm (21) and of Scheffer and Livingston (282), who showed that the decay fungi tested by them were able to continue normal growth at relatively low oxygen pressures, indicated that modification of Münch's views was necessary. Further evidence that oxygen supply is not likely to be limiting for true heart-rotting fungi has recently been supplied by Thacker and Good (308) in their investigation of the composition of gases in the trunks of sugar maple (*Acer saccharum*).

It has been amply demonstrated (80, 209, 308) that the composition of gases within trees may differ widely from that of normal air and that the composition varies at different seasons of the year and in different parts of a tree. Gas pressures within a tree may also show seasonal changes as well as diurnal fluctuations. A good many of the determinations of gas composition and pressure in trees have been made from specimens too young to contain appreable heartwood, or in such a manner that there could be no assurance that the gas samples originated solely in the heartwood. In the case of a single cottonwood (*Populus deltoides virginiana*) from which segregated samples were obtained throughout the year, Chase (80) found that the percentages of oxygen were much higher for most of the year in the sapwood than in the heartwood, while the opposite was true for carbon dioxide. CO_2 reached a maxi-

mum of over 25 per cent on August 1 in the heartwood, and was above 15 per cent for most of the time from August to November. During July and August, very low percentages of oxygen were present, and in one sample none at all could be detected. In December, however, the percentage rose rapidly to over 16, while the CO_2 content declined to a low level.

A distinct possibility that the values obtained by Chase may be abnormal arises from the fact that he is not known to have investigated the possible presence of wetwood, with its associated bacteria, in the cottonwood from which the gas samples were drawn. Wetwood is known to be extremely prevalent in cottonwoods (86), and the carbon dioxide evolved by the associated bacteria could be expected to produce abnormal gas compositions within the heartwood.

Thacker and Good (308) report much smaller differences in the carbon dioxide and oxygen contents of sugar maple. CO_2 content in the heartwood of nine maples sampled in June ranged from 1.9 to 4.8 per cent. Percentages from July samples were very similar. They found that the CO_2 content remained relatively high through the summer and early autumn but decreased markedly during the winter; also, that it was higher during the growing season in the heartwood than in the sapwood, in confirmation of Chase's earlier report to this effect.

Thacker and Good (308) appear to be the only ones who have investigated the composition of gases in decayed as against sound heartwood. They found that gas samples from decayed sugar maples averaged about six per cent higher in CO_2 and a corresponding percentage lower in oxygen than those from sound maples, although individual trees showed wide variations from these averages. The causes for the differences in gas composition between decayed trees were not explored.

From a comparison of gas compositions found by thm in maple trunks and their tests in vitro with different concentrations of carbon dioxide and oxygen on the growth in plate culture of fungi known to cause heart rots in sugar maple, Thacker and Good conclude that the composition of air commonly found in maple trunks during the growing season is nearly optimal for the development of such fungi. They noted a stimulation of fungus growth with increased amounts of carbon dioxide up to about ten per cent. Above

that level, growth reduction occurred, but growth was still appreciable at a 35 per cent concentration of the gas. Oxygen, in the percentages found by them in maples, did not limit the growth of any of the fungi tested. The authors (308) believe that their data " suggest that the idea of inhibition of decay fungi by ' poor ' aeration cannot at present be entertained, aeration in the tree appearing nearly optimal for decay ".

Whether this view can be accepted as a valid generalization for all tree species and all heartwood decays seems open to question. The fact that Chase (80) found much higher CO_2 concentrations in the heartwood of the cottonwood sampled by him than were encountered in maple by Thacker and Good (308), the demonstration by Bavendamm (21) that the growth of almost all fungi investigated by him was strongly reduced by a 19 per cent atmosphere of CO_2, and Zycha's finding (345) that percentages of CO_2 as low as 3 caused an appreciable slowing in the growth rate of *Fomes annosus,* all suggest limitations to the general applicability of the conclusions of Thacker and Good. Supporting this view are the observations already mentioned in a preceding section on the reduced rates of later progress of decays as compared with the rates of initial advance and the fact that they sometimes become completely arrested (133, 143, 189, 226, 275). Additional basic data appear to be needed before the question can be resolved.

EFFECT OF MOISTURE. In living trees there probably is always enough moisture in the heartwood to permit decay, and the only condition under which it becomes limiting is its presence in sufficient amounts to saturate the tissues and thus restrict the oxygen supply. In normal trees such a condition is likely to exist only during a few weeks in the spring (209), although in some species, for example, *Abies concolor,* accumulations of water may be present in the basal heartwood at almost any season of the year. Whether such accumulations are of pathological origin, as in wetwood (71, 86, 190), has not been determined, but, when present, they undoubtedly restrict the development of decay fungi.

EFFECT OF TEMPERATURE. Information on temperatures within the heartwood of trees is not extensive but is sufficiently definite and homogeneous to permit the conclusion that temperatures may often exert an important limiting influence on the rate of progress

of decay fungi within trees. Heartwood temperatures fluctuate less widely than air temperatures (256), and in the central heartwood of large thick-barked trees they change very gradually, approximating the course of a smoothed mean of daily mean air temperatures (18).

Practically all data on the temperature relations of decay fungi have been derived from measurements in the laboratory of the diameter growth of fungus colonies on agar plates maintained at different temperature levels. In a comparison of results obtained by this method with the biological activity of cultures of *Poria vaporaria* and *Schizophyllum commune* on wooden test blocks as determined by loss of weight, Gäumann (121) found that the maximum intensity of the decay process occurred at 2° to 3° C. lower than the optimum growth temperature on agar plates; but Cartwright and Findlay (77) believe that for practical purposes the optimum temperatures for growth in wood closely approximate those derived from colony growth measurements. This opinion is supported by the results of Rishbeth (260) who found that the rate of linear growth of *Fomes annosus* through lengths of pine root agreed well with growth rates on agar at similar temperature levels.

Optimum temperatures for most heart-rot fungi of Temperate Zone origin that have been investigated lie between 24° and 30° C. (77, 163, 310, 311), although one or two common ones, such as *Fomes annosus* (77, 260) and *Stereum sanguinolentum* (77), have optima between 20° and 23° C. The determinations of minimal temperatures for growth have been less well defined but appear to be about 4° C. for many heart-rot fungi (311), although Rishbeth (260) obtained a small amount of growth in *Fomes annosus* at 0° C. Temperature maxima for heart-rot fungi are somewhat more variable, but 35° C. is the approximate limit for many. From the standpoint of influence on the progress of decay within trees, they would appear to be of less significance than minimum or optimum temperatures because it seems probable that maximum limits are seldom exceeded within any except quite small trees or those growing in exceptionally hot regions.

In most forested regions of the world, except in the tropics and subtropics, heartwood temperatures will fall below the minimum for decay fungi at least part of the winter season, stopping all fungus growth, and for additional periods in the spring and fall

they will be low enough to permit only slow growth. In mountainous regions, moreover, internal temperatures in trees on shaded north slopes will average lower than in those on south slopes, and the period of complete or nearly complete inactivity of decay fungi that may be present will be longer.

Any close estimate of the effect that temperature might have on the activity of a decay fungus in the heartwood of a tree in any given situation would require an evaluation by some such means as a degree-hour summation within the temperature range for growth of the fungus from a continuous temperature record taken within the heartwood of a living tree, such as that reported for a ten-inch diameter cottonwood by Reynolds (256). So far, this does not appear to have been undertaken by anyone, leaving little basis for more than the generalization that temperature is quite certainly an inhibitor or retardant of the decay process in the heartwood of trees over a portion of each year in the Temperate or Arctic Zones.

EFFECT OF WOOD CHARACTERISTICS. Most of the experimental work on the effect of various wood characteristics on rate of decay has been carried out under controlled laboratory conditions, with loss of weight of test specimens within a selected time as the criterion of comparison. In the living tree, however, the relative loss of weight of the heartwood in the decay process is of less significance than the volume of wood affected or the lineal progress of the decay, since, for many purposes, the presence of decay in the heartwood, or in a major portion of it, causes the loss commercially not only of the heartwood affected but also of the sapwood and any unaffected heartwood in the surrounding portion of the trunk as well. Even where utilization as wood is not a consideration, as in orchard or shade trees, the linear progress of decay is likely to be more important than the intensity of the destructive action as measured by weight loss. Linear progress is difficult to compare under laboratory conditions, and accordingly field evidence on rate of progress from the heartwood of living trees of different wood characteristics is likely to be more useful than that obtained from most laboratory tests.

One of the most common differences encountered in wood structure is the difference in width of growth rings: wide in wood that has grown rapidly, narrow when the growth has been slow. From a review of laboratory studies up to 1943, Southam and Ehrlich

(300) concluded that no relation had been shown to exist between ring frequency and resistance to decay. The conclusions were based entirely on comparisons of weight loss in test specimens, however. Under natural conditions, when comparisons have been based on the relative progress of decay fungi in heartwood columns, progress has been found to be faster in rapidly grown trees with wide rings than in those with narrow rings that have grown slowly. This was found to be the case for decay fungi entering from broken tops (189) and from blaze wounds (98, 232) in spruce in Sweden, and for rot in balsam fir in northeastern United States (301). It was also true in Sitka spruce (32) in the Queen Charlotte Islands and in *Abies lasiocarpa* and *A. amabilis* (33) in the upper Fraser River drainage of British Columbia, even though the comparative rot percentages for fast- and slow-growing trees showed no consistent differences. The same applies to balsam fir (175) in the Lake States. The relationship is a consistent one, for if the decay rates in fast- and slow-grown heartwood were equal, the percentage of decay in slow-growing trees would be higher than in those that had grown rapidly. Occasionally this is found to be the case, as reported by White (328*a*), for eastern white pine in parts of Ontario. Other evidence (42, 46*a*, 99, 320, 343) supports the probability that more rapid progress of decay in fast- than in slow-grown wood is general in conifers, although Haufe (136) found no difference in the amount of decay present in fast-growing as compared with slow-growing spruces wounded by red deer in Saxony. Scheffer and Englerth (278) found no difference in the decay resistance of the heartwood of second-growth Douglas-fir from Site II, where growth was relatively rapid, as compared with Site IV where growth was slow, and the relationship has not been demonstrated to exist in hardwoods (142, 275, 285), in which rate of growth has a less pronounced effect on wood characteristics, especially in species with diffuse-porous wood (48).

A commonly used basis for the comparison of wood for technological purposes is that of specific gravity or weight, which in conifers usually varies according to the percentage of summer wood in the annual rings and with ring width, fast-grown wood with wide rings tending to be lower in specific gravity than wood with narrow rings. In hardwoods the relationship is usually reversed. However, there are many exceptions. Slow-growing wood from old

trees tends to be lighter in specific gravity than average (48), and Gäumann (124) has found that in larch in Switzerland both ring width and specific gravity showed a pronounced decrease with elevation above approximately 1100 meters. From the fact that some woods with high specific gravity have been found to be very durable, there has been a tendency to conclude that this relationship is a general one, but specific evidence fails to support this conclusion (300).

One might anticipate a more rapid progression of decay in hardwood tree species characterized by ring-porous wood in which the pores (vessels) ordinarily remain open, as in *Quercus velutina* or *Q. coccinea,* than in those in which the vessels become blocked by tyloses, as in *Q. alba,* because of the unobstructed paths for extension of the fungus hyphae provided by the open vessels. Laboratory tests (279) and field evidence (275) support general experience that the heartwood of oaks of the red oak group, which have open vessels, is more rapidly decayed than that of the white oak group in which the vessels become closed. However, there appears to be no reliable evidence that the difference can be ascribed to the open condition of the vessels in the red oak group. As Scheffer and associates (279) pointed out, some specimens of red oak heartwood prove to be just as durable as the average from white oak, which would hardly be the case if the mean differences between the decay resistance of the two groups rested primarily on the condition of the vessels. It would appear, instead, that these differences rest on the nature of the heartwood substance in the respective groups or the relative toxicity of the hot water extractives, which, according to Zabel (340), appear to belong to the tannin complex in white oak. Hunt and Garratt (164) believe that the relatively poor durability of the heartwood of some of the open-pored species of oaks, such as those in the red oak group, under service conditions where they are exposed to free moisture, may be ascribed to the greater ease with which leaching of the water-soluble extractives may take place, because of the open structure, as compared with species in which the vessels are closed. In the living tree, however, leaching should not be a factor.

EFFECT OF INFILTRATED OR DEPOSITED MATERIALS. The influence of the protective substances deposited in heartwood during its formation on the establishment of decay fungi and on their subse-

quent progress differs widely in different genera and species of trees and even between different geographic races or different individuals within the same species (279, 280, 281, 340) This is to be anticipated from common experience concerning the wide range in durability between various heartwoods in use (164), although resistance to decay fungi commonly attacking forest products may not connote a similar degree of resistance to all heart-rot fungi that may attack the living tree. Because of the presence of toxic thujaplicins (102), the heartwood of western red cedar is quite resistant to attack by ordinary decay fungi, but in the living tree *Poria weirii* is able to decay the heartwood in spite of the thujaplicin content. The same is true for a number of other specialized heartwood-destroying fungi causing decays in other tree species with heartwood rated as durable—e.g., in black locust.

The heartwood components conferring resistance to attack by decay fungi are usually either constituents of volatile oils, as that from Port Orford white-cedar (*Chamaecyparis lawsoniana*) (334), or fall within the tannin complex. The most active constituents fungicidally or fungistatically are often phenolic in character, as pinosylvin (101, 251), the thujaplicins (102) and chlorophorin (132). As a rule, they are water-soluble and extractable by leaching, especially with hot processes (137).

Within the heartwood of individual trees, decay-resistance gradients have been demonstrated for redwood (292), Scotch pine (253), oaks (279, 340), European larch (74), western red cedar (73) and black locust (280), and in four tropical hardwoods with visibly differentiated heartwood (277). In these the most resistant wood at any particular cross section was found to be next to the sapwood, and the least resistant near the pith. In most of them durability also decreased from the basal heartwood toward the top of the tree, although in European larch Gäumann (124) found that on the average the heartwood six to seven meters above ground was more resistant than at one meter, and in four eastern American oak species Scheffer et al. (279) found the heartwood at comparable positions in the upper trunk more resistant than in the lower. As a result of determinations from white oak heartwood, Zabel (340) demonstrated that both the amount and concentration of tannins extractable by hot water are variable and concluded that decay resistance in any particular part of the heartwood is probably

determined by the joint effect of both variables. Along individual radii in trees greater variation was found in the toxicity than in the amount of extractives present. However, as a rule, hot water extractives provide an index only of gross differences in decay resistance, and accordingly it seems questionable to what extent conclusions can be drawn from them alone.

Zabel believes that the lower toxicity of the extractives in the oldest heartwood near the center of the tree, as compared with that most recently formed next to the sapwood, suggests that a gradual decrease in toxicity of tannins occurs with age in oak heartwood. Scheffer and Hopp (280), from tests with black locust, agree that the decay resistance of heartwood at any one point does not remain constant but decreases as the tree becomes older and larger. However, they were uncertain whether this loss in resistance resulted from deterioration of the protective substances present or from their partial migration to outer portions of the heartwod cylinder. Whatever the explanation, the reduction in decay resistance with age in the center heartwood provides an additional explanation, besides the cumulative risk from wounding, etc. (17, 216), and the higher proportion of heartwood present (196), for the increased prevalence of decay with age in trees—a relationship that is well marked in practically all species (17: p. 164).

The differences in decay resistance found to occur between varietal clones of black locust and the common form (280), and the wide differences in this characteristic found to occur between individual trees, indicate that they are of genetic significance and that advantage may be taken of individuals with highly durable heartwood in the selection and propagation of planting stock. While the genetic behavior of antibiotic substances conferring durability on heartwood has not yet been proved, there is no reason for believing that the faculty for formation of these antibiotics will not be transmitted in a normal manner, offering the possibility of the development of stocks with highly durable heartwood through breeding. Scheffer and Hopp (280) offer suggestions for the sampling of black locusts for heartwood durability in a selection program. The demonstration of these individual differences in susceptibility to heart rot between trees and races or clones also raises a question concerning the advisability of leaving, for seed production, trees defective because of decay, as has sometimes been done in Douglas-fir in the

Pacific Northwest (43, 320) and as is recommended for Oregon by Boyce and Wagg (46*a*) for compliance with the State law regarding the leaving of seed trees. Because of the dropping out of defective Douglas-firs before the stand reaches a high age (46*a*, 320), a certain amount of natural selection undoubtedly has taken place in the virgin stands of this species as it has in Sitka spruce (32), leading to a higher average resistance to the chief heart-rotting fungus, *Fomes pini,* than would be likely if the greater part of the new growth originated from seed from defective trees. The practice currently in use in much of the Douglas-fir region, of deferring the cutting of prominently located blocks of virgin timber to serve as seed sources for surrounding clear-cut land, escapes this objection.

CONDITIONS INFLUENCING PROGRESS OF DECAY IN STANDS

Among the basic determinants of defect from heart rots, as listed by a committee of the Canadian Institute of Forestry (113), are age, stand history, stand composition and site. To these may be added the influences of climate and topography for the part they play in determining environments that may greatly affect the establishment and progress of decay, as the discussion of the means of entrance of decay fungi and of the conditions affecting the progress of decays in individual trees has indicated. With any of these factors, the influence may be indirect and the relative effect of one may not be separable from that of the others. The vigor of trees, for example, through its effect on the characteristics of the wood produced and on the rate at which wounds are healed and knots grown over, may have a definite influence on decay; but vigor, in turn, may be the joint result of the effect of genetic inheritance, age, soil characteristics, moisture supply, the competition of surrounding trees, and other influences.

AGE OF STAND. For readily understandable reasons, most of which have already been mentioned, one of the most consistent relationships that has been demonstrated in investigations of heart rots in individual tree species in timber stands has been that of the increase in number of decay cases and in volume of decay with increasing tree age. Heartwood is absent in very young trees, and later when it forms, at ages depending on tree species and rate of growth (95, 241), it is initially well protected by the sapwood and there are few opportunities for the heartwood-attacking fungi to gain entry. With increasing age, as previously noted, opportuni-

ties for infection multiply (207), the relative proportion of heartwood increases, the rate of healing of wounds becomes slower and the resistance of the center heart to decay decreases—all contributing to increased decay percentages with increasing age of the stand (Figure 1).

Among the species in North America for which a pronounced relationship between tree age and decay volume has been shown are balsam fir (175, 207, 301), other firs (33, 51, 54), Douglas-fir

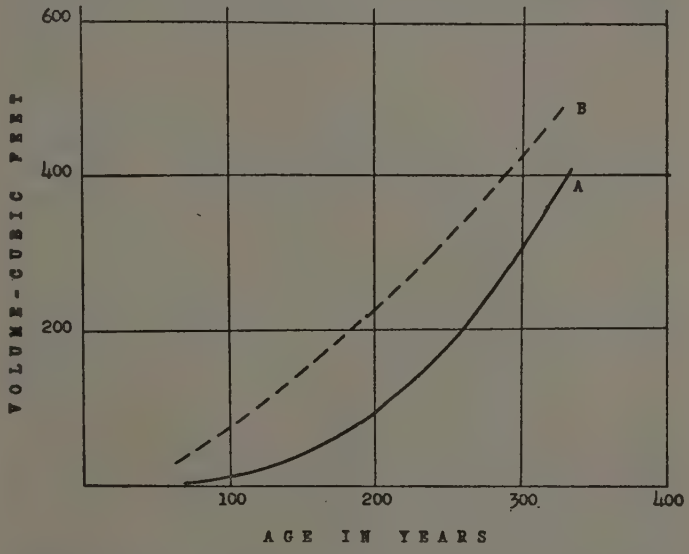

FIG. 1. Increase in cull from decay with tree age in white fir, northern California and southern Oregon. A. Average cull volume from decay in cubic feet. B. Average gross tree volume in cubic feet.

(45, 46*a*), incense-cedar (41), Sitka spruce (32), western hemlock (51, 54, 99, 112, 323), eastern white pine (328*a*), western white pine (324), aspen (216, 257*a*, 285), oaks (149, 275) and yellow poplar (149). In the managed stands of Europe there has not been the same need for determining the decay relationships as in the New World, but results, such as those reported by Schober and Zycha (287) for larch in northwest Germany, the volume distribution by age classes of pines infected with *Fomes pini* cited by Röhrig (268) for the Potsdam region of East Prussia, and the

increase in decay with diameter, closely correlated with age, in pine and spruce in Sweden (36), indicate that the relationship with age is a universal one.

STAND HISTORY.—What may be termed the normal age-decay gradient for a stand may be strongly influenced by events in the stand history, such as the occurrence of fires or of unusually severe sleet storms, or by the silvicultural conditions under which the stand has grown. In forests subject to ground fires, the wounds produced during single bad fire years may play a predominant part in the subsequent course of development of decay in the stand. Thus Hepting (142) found that most of the fire wounds on black oaks studied in the Mississippi delta originated during the two fire seasons 1917–18 and 1924–25, and in consequence the height reached by decay in the trunks showed only a slight correlation with tree age when other factors were held constant. In contrast, where recurrent fires have been suffered over a long period, as in the mixed conifer stands of the Sierra Nevada (186, 295), heart rots show a normal age gradient (41).

Where the principal heart-rotting fungus present is a species that ordinarily enters through dead branches other than very small ones, as is the case with *Polyporus anceps* in the ponderosa pine forests of southwestern United States (6), it is evident that the density of the young stands, which in turn will determine the diameters reached by the side branches before they die, will at the same time be a major determinant of the establishment of heart rot. Under some conditions the thinning of stands may be accompanied by an abnormal increase in the amount of butt rot, as reported for white pine plantations by Hepting and Downs (147) and for Scotch pine by Rishbeth (261). On the other hand, failure to thin balsam fir in the New England States may result in suppression leading to a flat-topped form that favors infection by *Stereum sanguinolentum* (301, 344). Wounds resulting from logging may be the source of increased heart rot in residual stands of species such as western hemlock and Sitka spruce (336). Nordin and Cafley (233) attribute the high cull per cent from decay in hard maple in Sherbourne Township, Ontario, to poor site conditions and an unfavorable stand history. Haufe (136) stated that wounds from red deer are few in Saxony spruce stands over 100 years old, but that in younger stands wounding by them is sometimes so common and the

resulting rot so serious that early cutting and regeneration will be necessary.

These few illustrations, and others cited in the section on "Establishment of Heart Rots", should be sufficient to demonstrate the importance that the history of the stand and the silvicultural treatment that it has received are likely to exert in determining the amount of heart rot present and the age relationships that have developed between it and the stand. Except for those traceable to variations in environment, the explanation for many of the differences that occur in decay percentages within the same tree species on different areas is to be found in the histories of the respective stands.

STAND COMPOSITION. Except for subclimax species that commonly seed in following catastrophes such as crown fires, as exemplified by aspen, lodgepole pine and Douglas-fir, and for pure stands established by planting, even-aged forests of a single tree species are seldom encountered. Stands of uneven age or of mixed species are much more common (17). We have already seen that tree species vary greatly in their susceptibility to decay and in the rate of increase of decay with age, and also that almost invariably old trees are more defective than young ones. It follows that the percentage of defect to be anticipated in a mixed stand will be a composite of the decay percentages contributed by the individual species components of the stand, and the amount of each of these will be governed by the age classes representing the bulk of the volume in each. In 47 acres of study plots in the Queen Charlotte Islands of British Columbia, Foster and Foster (112) found that, although western hemlock, Sitka spruce and western red cedar were represented and that 38 per cent of the volume of the latter was decayed, the average decay percentage for the stand was 25.2, very close to the average for the western hemlock, which predominated on the plots.

The future decay potentialities of a stand may be increased by cutting practices that favor tree species susceptible to decay. One of the strong arguments against the selective cutting of Douglas-fir on the Pacific Coast, as contrasted to clear-cutting in blocks or strips, is the fact that selective cutting not only leaves a residue of understory hemlock or true firs in which decay is likely to become established through logging wounds (336) and which are inher-

ently more defective than Douglas-fir, but also favors future establishment of these other species (228). Foster and Foster (112) point out that in the Queen Charlotte Islands 97 per cent of the understory trees on their plots were western hemlock. Thus, unless cutting could be made to favor the associated Sitka spruce and western red cedar, the future stand will consist almost entirely of hemlock, in which decay becomes common at a much earlier age than in Sitka spruce (32, 112).

Various European investigators (94, 185, 246, 254) have recommended a change from pure coniferous to mixed-conifer-hardwood stands as a means of reducing the damage from butt rots, and Röhrig (268) has offered the opinion that a mixture of beech in Scotch pine stands, along with controlled densities, will assist in reducing the danger of infection from *Fomes pini.* In a survey of spruce stands in Sweden for rot from *Fomes annosus,* Rennerfelt (254) found that, as a rule, spruce mixed with hardwoods was less affected by rot than where it occurred in pure stands. Falck (105) and Peace (238), on the other hand, from surveys of spruce in the Harz Mountains of Germany and of various conifers in England, respectively, found less butt rot in pure than in mixed stands, while Schober and Zycha (287) could find no difference in the frequency of decay cases in pure stands of larch in northwest Germany, as compared with mixtures with beech or other deciduous species. In balsam fir in eastern Canada, Heimberger and McCallum (140) report a fairly distinct positive correlation between butt rot from *Poria subacida* (probably largely from *Corticium galactinum* and *Odontia bicolor* (19)) and the proportion of hardwoods in the stand, while for brown butt rot from *Polyporus balsameus* the correlation was not as distinct. In general, the frequency and intensity of butt rot of both types was greater on mixed-wood slopes than on softwood flats. Limited observations on rots in white spruce indicated a negative correlation with the proportion of hardwoods. The higher frequency of butt rot on mixed-wood slopes has been confirmed by Basham and co-workers (19). Increased decay with increasing purity of stand is reported by Boyce and Wagg (46*a*) for Douglas-fir in southern Oregon, but the purer stands occur on the better sites, and decay also was found to increase with site quality. They were unable to determine which relationship was the more significant. Stands in which incense-cedar was a component were found to be highly defective.

One of the best-controlled examples of the advantage of mixed over pure stands is reported by Flury (110) from Switzerland. Two equal-aged neighboring plots, one of pure spruce and the other of alternating rows of spruce and beech, were compared for rot from *Fomes annosus* in the spruce. In 1909 the number of trees affected was found to be four times as great in the pure as in the mixed stand. Decay in the mixed stand was negligible in volume, but amounted to 2.7 per cent of total merchantable volume on the pure plot. By 1923 the per cent of trees affected was nearly as great in the mixed as in the pure stand; but the decay volume in the pure stand was still more than double that on the mixed plot. The difference on these plots was attributed to the effect of the beech on the physical condition of the soil.

The probabilities are that no valid generalization can be made regarding the influence of pure as against mixed stands on heart-rot incidence. The recommendations by König (185) and Priehäuser (246) for conversion to mixed stands were made to apply to specific situations in which unfavorable soil and biotic conditions were major considerations and were not advocated for all pure stands under all ecologic conditons. On the area dealt with by Priehäuser, the unfavorable conditions resulting in increased butt rot became significant only after the stands had become fairly old and more open, and were not operative while they were young. Surveys confined to young stands might therefore lead to erroneous conclusions regarding the advisability of favoring pure species compositions.

Even where a mixed stand results in a greater incidence of rot than if it were a pure stand, there may be silvicultural advantages in maintaining the mixed composition. Thus, Spaulding and Hansbrough (301) show that upland stands, which contain more hardwoods than those on flats, give greater net yields of balsam fir up to about 80 years than do stands on flats, even though the cull percentages on uplands are greater.

SITE. The term " site ", as commonly used by foresters, refers to the capacity of an area for forest growth. It usually is judged by the height growth made by the trees present. A number of investigators of heart rots have included forest site quality ratings in their collection of data, although in general there seems little reason for anticipating any very significant or constant correlation between site quality, based on tree growth capacity, and percentage

of decay at a given age. Falck (105) found no appreciable difference in rot per cent in spruce on sites of different classes in the Harz Mountains, although the per cent of trees infected with red rot was higher on the better sites. Englerth (99) in western hemlock in western Oregon and Washington was unable to demonstrate any pronounced relation between decay volume and site class, but in Douglas-fir in Oregon, Boyce and Wagg (46*a*) found that trees were infected earlier and the percentage of infected trees was higher on the better than on the poorer sites above a stand age of 110 years. In younger stands the relation appeared to be reversed. Foster and Foster (112) stated that "Progressively smaller cull factors were encountered with increasing site quality", but the comparison was based on diameter rather than age, and the two showed wide deviations. Foster and Craig (111) reported a higher cull loss on the lower of two site qualities in western hemlock in interior British Columbia, but expressed skepticism as to its significance. Spaulding and Hansbrough (301) found an appreciably greater percentage of cull in balsam fir on poor than on good sites. In summation of studies in which decay has been compared on site indices based on tree-growth capacity, some tendency has been shown for decay to be greater in proportion on poorer sites, but the relationship is far from being pronounced or consistent.

Where stands have been compared on other than a height growth index basis, differences in decay have been noted in some cases and not in others. No difference was found between bench and slope types in Sitka spruce on the Queen Charlotte Islands (32), and no appreciable difference in balsam fir in ridge and swamp types in the Lake States (175). In western white pine in Idaho (324) and in red spruce in New York State (240), more decay was found in trees on bottoms or flats than on slopes. The same was true at comparable ages for western hemlock in the Inland Empire region of northwestern United States (323). The younger age classes of incense-cedar in the intermediate range of the species in California were found to contain more decay than trees of similar ages in the optimum range (41), and jack pine in the Lake States was observed to contain more rot in the moister portions of its range, where it occurred in mixture with other species, than in pure stands on the drier sites (322). Spruce in the Harz Mountains of Germany contained more rot on north than on south slopes, and the

steeper the slope the greater the per cents of rot and infected trees (105). The opposite has been reported for Sitka spruce in Denmark (198), and in England no correlation was detected between rot and slope in spruce, while other species tended to be more sound on the steeper slopes (238). *Fomes pini* rot is reported as more prevalent in Scotch pine in eastern Germany, where precipitation averages less than 600 mm. (23.6 in.) per annum, than in western Germany where it exceeds this amount (196), although no evidence is given that the rainfall difference is responsible for the difference in decay. Similarly, rot from *F. pini* is reported to be heavier in Douglas-fir in central and southern Oregon, where annual precipitation is less than 60 in. (1525 mm.), than in other parts of the Pacific Northwest where precipitation is greater (320). It was found to be greater on southerly than on northerly aspects, on steep slopes than on gentle ones, and on ridge tops than on bottoms or benches. These differences are believed to be basically related to temperature (46*a*). In England a definite inverse relationship was found between rainfall and number of rotted trees in larch, but not in other species (238). The generally sound condition of Philippine hardwoods in northern and central Luzon, as compared with the more defective state of those in the southeastern portion of the Island, is attributed to the longer dry season prevailing in the northern and central parts (337).

Comparable differences are found in the reported relationships between soils and heart-rot incidence. For example, Brown (49), using the plot data of Schmitz and Jackson (285), was able to find no statistical evidence that percentage of rot in aspen in the Lake States varies with soil types; but Stoeckler (304), from field studies of site factors in the same region, shows a decided relationship between soil character and the age at which culmination of net growth in aspen occurs, after which it begins to decrease because of rot and mortality. According to Wilfong (330), oak with the same fire history is much more defective on poor than on highly productive soils. In Sweden, Rennerfelt (254) found very little rot in spruce on peat and moor sites, but it was common on upland soils characterized by *Vaccinium* associations, and heavy attacks were seen on permeable and dry soils. However, no relationship could be found between soil character and occurrence of *Fomes annosus* rot. On the other hand, Falck (105), in the Harz region,

recorded a higher rot per cent on shallow soils derived from granite, quartzite, sandstone and siliceous shale than on deep soils of these origins, whereas there was no difference between the amount on deep and shallow clay soils. Peace (238) in England found rot the worst on clay soils and least on sands, while in larch the relations were reversed. He obtained no correlation between the amount of rot and depth of soil. No relation could be established by Schober and Zycha (287) between soil type and butt rot of larch in northwest Germany. On one point most investigators are in agreement: Rot is likely to be more severe on ground formerly under cultivation (157, 185, 198, 238, 254, 255*a*).

From the standpoint of observed association, Fenton (108) has reported more prevalent heart rot in Scotch pine where the moss, *Leucobryum glaucum,* is abundant in Britain and a less marked relation with the presence of the grass, *Holcus mollis.* In Oregon, Boyce and Wagg (46*a*) report that a high incidence of rot from *Fomes pini* in Douglas-fir was associated with the presence of vine maple (*Acer circinatum*) and *Oxalis* spp., while the incidence was low where *Rhododendron* was present.

It seems evident that, in the aggregate, a very large amount of effort has been devoted to the recording of observed correlations between decay incidence and site, or its features or indicators, without the emergence of any consistent, clear-cut or widely applicable general relationships. One would be in error, however, in concluding from this that site, in the broader sense of the environment rather than in the more limited foresters' sense, is of questionable importance in its influence on decay. What has been lacking in most of the investigations where correlations have been found has been any attempt to establish the fundamental reasons for the observed relationships or to separate the influence of environment from others that may have had a part in bringing about the decay status found in the particular stands under study. There is reason to believe that when the fundamentals have been sufficiently explored they will provide a foundation that will permit a better appreciation of the effects of site.

A growing realization of these shortcomings and of the need for the development of site criteria on an ecological or what may be termed a pathological basis is developing (111, 320). A basis of this sort would require a synthesis of two main elements: the environmental or other conditions inimical to or favoring establish-

ment of heart-rot fungi in the host, and the influences affecting the progress of such fungi after establishment. Contributing to the first of these should be a knowledge of the ecology of sporophore production of the principal heart-rotting fungi. A substantial beginning has been made, chiefly by investigators in England and in central Europe, in the study of the ecology of the higher fungi (84, 85, 85*a*), but has been directed almost entirely toward sporophore production in saprophytic forms, particularly in the Agaricaceae. While an understanding of the ecology of the saprophytic forms will unquestionably be of help in reaching a similar understanding of the influences regulating sporophore production in the heart-rotting forms, there is a need for directing investigation specifically toward the latter groups and toward the ecology of fungus establishment rather than merely sporophore development. The observations of Hepting and Roth (151) on the fruiting of heart-rot fungi on felled trees are of introductory value toward this end.

For fungi that primarily cause trunk rots, such as *Fomes pini* and *Polyporus anceps,* climatic conditions are certain to play an important role in the determination of pathological site. An excellent example of this is afforded by *P. anceps* in ponderosa pine. This fungus, which normally gains entrance into the heartwood by first establishing itself as a saprophyte in dead branches and spreading from these inward through the branch knots (5), causes from 10 to 50 per cent cull in ponderosa pine in Arizona and New Mexico (6), whereas in this species in California *P. anceps* is infrequent and total cull is low (180). The difference can be ascribed with reasonable certainty to a difference in climatic conditions in the two regions (6, 23). The pine areas of Arizona and New Mexico enjoy a summer rainy season (239), sometimes with moderately high relative humidities, which permits the establishment of *P. anceps* in bark-covered dead branches. In contrast, summers in the pine region of California are dry (8) and humidities too low to allow development of *P. anceps* in attached dead branches.

An attempt to analyze site factors on a more fundamental basis for Douglas-fir in southern Oregon is reported as under way (320).

PHYSIOLOGICAL EFFECTS OF HEART ROTS ON THE HOST

Very little appears to be available in the literature on the possible physiological effects of the presence of heart rot in a tree trunk on the physiology of the host. Aaron (1) holds, without supporting

evidence, that " heart rot will interfere in a cumulative manner with normal development, through retardation of the developmental processes, with consequent reductions and changes in the amounts and types of tissues that form ". He also believes that heart rots, by reducing the capacity of the heartwood to act as a water reservoir, secondarily interfere with conduction in the host.

Against these views, Meinecke (214) found that very thrifty white firs were sometimes badly decayed by *Echinodontium tinctorium* without any apparent diminution in growth rate, and Englerth (99) concluded that there was probably no connection between reduction in thriftiness and the presence of heart rot from this fungus in western hemlock. Wagg (320) reports slower growth and probable earlier mortality in Douglas-firs badly decayed by *Fomes pini,* but this fungus may affect the cambium and sapwood as well as the heartwood proper (196) with apparent advance lethal action preceding actual invasion (133), and this, instead of any action as a true heartwood-destroyer, may account for the gradual debilitating effect on the host. Christensen (82) states that *Polyporus circinatus* is likely to be a primary cause of stagnation in growth and senescence of white spruce, but this conclusion is questioned by Gosselin (129) who found that the average age of infected trees was greater than that of sound ones. In any event, a deleterious effect by this fungus on the host would more likely be brought about by the destruction of roots than through any function purely as a heart rot. Eide and Christensen (97), from observations in apple orchards in Minnesota, believe that rot may be one of the causes of the early decline of apple trees there; but winter injury and the observed direct pathogenic action of the heartwood-destroying fungi present prevented any clear-cut conclusions as to the physiological effect on the host of the heart rots as such. It seems clear that some fungi occurring chiefly as heart rots may also act as direct pathogens in bringing about a decline of the host, but to date a deleterious physiological effect on the host from the presence of decay in the heartwood does not appear to have been satisfactorily demonstrated.

ESTIMATION OF DECAY IN LIVING TREES

Means for detecting and appraising the extent of heart rots in trees are useful to the forester in estimating the probable amount of defect in timber stands, to the orchardist in pruning and in

reaching decisions concerning replacement of senescent trees, and to the arborist or park forester in judging probable hazards to life or property from trees weakened by decay and in reaching decisions on tree maintenance. They are especially important in forestry when timber is sold on a tree-measurement basis (158, 194).

In the estimation of heart rots, advantage is commonly taken of various indicators of their presence. These fall into two classes: (*a*) openings or scars indicating the presence of former openings providing favorable avenues for the entrance of decays, such as wounds from various causes, cankers, or large branch stubs; and (*b*) signs of the presence of the decay fungus, such as sporophores, swollen or abnormally colored knots, swollen tree bases and resin flow. In addition to indicators that are present, other aids are sometimes employed to advantage in diagnosis, such as the sounding of trunks by pounding on the bark with an axe (2, 44, 158), extraction of sample cores by means of an increment borer (158, 254, 315, 316) and X-ray examination of tree trunks (248). Successful use of chisels mounted on long handles for testing the presence of infected knots in Scotch pine where *Fomes pini* rot was suspected has been reported (96). In spruce it has been found possible to judge the amount of rot in wounded trees rather closely by the appearance of the wounds (136). In hardwoods the evidence of sprout or seedling origin of trees is often of value in estimating the probability of decay (130, 149, 233, 275); in sprout stands, butt rot is less apt to occur in sprouts starting at or below ground level than in high origin sprouts, and sprouts from small stumps are less likely to be decayed than those from large stumps (273, 275).

Indicators have been used successfully in estimating decay in Douglas-fir (45, 46*a*, 320), oaks (143, 148), Rocky Mountain conifers (158) and redwood (181), and in detecting decayed Scots pine (96); but in some stands, such as white pine in northern Ontario (133), jack pine in the Lake States (315), shortleaf and loblolly pine in southern United States (146), Sitka spruce and western red cedar in British Columbia (29, 32, 53), and spruce in parts of Sweden (254), they have been found to be inadequate as an index of the decay present. As a rule, estimates of defect based on them are not likely to be accurate when applied to individual trees, but must be averaged for stands or stand samples to be applicable within satisfactory tolerance limits (45, 46*a*, 126, 158, 180, 181).

The size of sample needed is determinable by statistical methods (342), and for specific purposes may be determined by formula (126). Because of differences in the relationship between indicators and decay that may occur over a large region, criteria that may give very close approximations to actual cull from heart rots in some districts may yield much less satisfactory estimates when applied in others (46*a*, 320).

General rules based on indicators, such as those developed for cull in northern hardwoods in New England (302), are very helpful in the cruising of timber, but the tendency in recent years has been toward the grouping of indicators into defect or risk classes (126, 148, 180, 342) and toward derivation of cull factors or percentages deductible from gross volumes of trees to obtain the net merchantable volumes (126, 180). These may be based on indicators, or, in species in which cull is low or cannot be satisfactorily judged from indicators, they may be expressed as flat factors, applied without reference to the presence of wounds or other signs of decay by diameter classes (180, 181).

Trustworthy cull factors for heart rots must be based on the analysis of felled trees selected to comprise reasonably adequate samples of the stands to which the factors are to be applied and without wide diversity in decay relationships. The significance of variability among samples may be tested statistically (143). The inadequacy of information based on small local samples as a guide for estimation of decay in a species represented over a wide geographical area is illustrated by the cull data obtained for western hemlock in the early study of this species by Weir and Hubert (323) as compared with that later provided by the studies of Englerth (99), Buckland et al. (54), Foster and Craig (111), Browne et al. (51) and Foster and Foster (112) in other parts of its range. Not only were decay volumes for comparable ages or diameters found to be quite different in different portions of the range, but also the species of fungi predominantly responsible for the decay. Because of the likelihood of differences such as these, Bier and co-workers (32) warn against applying results of their study of decay in Sitka spruce in the Queen Charlotte Islands to the species in areas outside these Islands.

By sampling with an auger or increment borer, internal criteria may sometimes be used as guides in determining the deduction to

be applied to gross volumes because of heart rots. Brown (49), by the statistical analysis of sample plot data for aspen in Minnesota collected by Schmitz and Jackson (285) and others, found that the diameter of rot in dominant trees at one foot from the ground gave as accurate an index of the rot percentage in the stand as any other criterion and was simpler to apply. However, it was applicable only to estimates in cubic feet or cords, and not to those in board feet. Use of increment borers for decay determinations in forest trees has been reported also by Rennerfelt (254), Hornibrook (158) and Varner (315), and has been recommended for determination of the extent of decay in shade trees by Vaughn-Eames (316).

For decay resulting from a single catastrophe, such as a fire, Hepting (143) has developed a formula for prediction of cull in oak in the Appalachian Mountains of eastern United States at any year after formation of the entry wounds. These may be expressed in the form of curves of cull volume by wound widths over age of the basal wounds.

LOSSES FROM HEART ROTS

The chief significance of heart rots from the practical standpoint lies in the destruction of usable wood occasioned by them. This loss is cumulative, usually recognizable without particular difficulty when trees are cut and opened up, and lends itself well to measurement. Technical advantage is taken of these features. According to Chester (81), " In only one branch of plant pathology has the determination of present and future disease loss become well developed. This is in forest pathology, where accurate estimation of wood-decay volume has gained leading importance in determining optional cutting cycles and in appraisal of present and potential sales value of the crop ". The very substantial capital investment required for the establishment of a modern logging and milling operation, the increasingly important part played by transportation costs in logging and the marked increase in the stumpage values of timber in recent years have made accurate assessment of the loss factor in forest stands tributary to a lumbering operation much more vital than was formerly the case (180, 312). Over-mature stands of some forest species may be so defective that harvesting is financially impracticable. For the forester concerned with the

growing forest, accurate anticipation of losses to be expected from heart rots over the course of a rotation is also vital because it is on the net volume of usable wood produced that the success of the operation depends. In fields other than forestry, heart rots may shorten the productive life of orchards (97), render trees more susceptible to storm damage (218) and may at times result in public hazard in park and street trees.

Losses may be expressed either in terms of the wood volume rendered unmerchantable or in the monetary value represented by it (146, 312). These vary greatly in different parts of the world, depending on tree species, the status of wood supply and use, and the conditions influencing decay incidence and development. In virgin forest stands the loss rate in volume is usually much higher than in growing managed forests, such as those in much of Europe, because of the high average age of the trees in virgin forests and the absence of sanitation or preventative measures against decay.

In contrast to losses from fire, storms and epidemics of killing diseases or insects, which tend to be sporadic or catastrophic, those from heart rots are characterized by much greater uniformity and continuity, disturbed only by destruction of the trees or stands in which they are taking place. For the United States the annual loss of wood due to cull from decay in saw-timber stands of all commercial species has been estimated at more than 1.5 billion board feet per year, with an estimated stumpage value, based on average 1943 stumpage prices, of something over nine million dollars (312). Current stumpage prices are very much higher than those of 1943, and current estimated values would need to be increased accordingly (313). Actual loss values of cull from decay are probably higher than those based on stumpage prices because some of the cull is not eliminated until the defective logs are sawn, and felling, logging and sawing costs are thus incurred on the cull material (312). Total estimated cull in saw-timber stands, by principal species or types, for the United States is shown in Table I.

No comparable estimates of loss of such a comprehensive nature appear to be available for forests in other parts of the world, but in the Potsdam region of Germany, over 1,100,000 pines, with a gross volume of 263,940 cubic meters, were removed during the three years 1928–30 in the course of a sanitation program to rid the forests of sporophore-bearing trees of *Fomes pini* (268), while in northern Sweden an average of 2.8 per cent of the conifers are

damaged by decay (36). Locally in spruce in Sweden, up to 85 per cent of the trees may be defective (254). In the Harz region of Germany, merchantable volume loss from red rot for an area of 412 hectares (1018 acres) amounted to 10.2 per cent, with a value loss of 7.6 per cent (105). Cull from rot in hardwood logs in

TABLE I

GROSS TIMBER VOLUMES AND ESTIMATED CULL LOSSES IN PER CENT FROM HEART ROT IN STANDING SAW-TIMBER, UNITED STATES, 1945

(Adapted from Report 5, A Reappraisal of the Forest Situation, U. S. Forest Service, 1947)

Species	Gross volume, million bd. ft.	Per cent cull from decay
Eastern hardwoods:		
Oak	125,162	19
Beech, birch, maple	85,933	21
Redgum	30,432	13
Yellow-poplar	14,357	14
Cotton and aspen	17,798	12
Others	91,509	18
Eastern softwoods:		
Southern yellow pine	194,152	3
Hemlock	16,956	12
Spruce and fir	29,678	9
White and red pine	16,193	5
Cypress	7,513	17
Others	8,710	11
Western softwoods:		
Douglas-fir	505,915	15
Ponderosa pine	193,168	4
Western hemlock	121,509	20
True firs	138,465	18
Redwood	42,349	10
W. white/sugar pine	42,791	6
Lodgepole pine	23,978	8
Spruce	40,773	12
Others	93,340	20
All species	1,840,681	13

northern Mindanao, Philippine Islands, exclusive of cull logs and trees left in the woods, was found to range from seven to 31 per cent, according to species (291), and in southeastern Luzon, about 14 per cent on the same basis (337). It is evident that rot has been an important source of loss of accumulated wood capital in practically all forested regions of the world.

AVOIDANCE OR REDUCTION OF HEART ROTS

Because of the relatively rapid reduction in area of the virgin, often over-mature, softwood forests of the world, as a result of cutting, together with the effects of shifting cultivation, fire and logging on the extensive hardwood forests of the tropics and semi-tropics (294), it is probable that the total volume of heart rots, considered globally, is gradually diminishing. But, as the defective virgin forests are reduced, the value of trees and of wood increases (313), imparting an increasing significance to the losses from heart rots and an increasing necessity for preventing them as far as possible in our growing trees, whether in the forest, the orchard, or around our homes.

Decay control methods feasible for forests differ from those for orchard, shade or ornamental trees in that they must usually be applied on a stand basis rather than to individual trees. Even at the highest of current stumpage values, forest trees cannot bear the financial cost of individual care, such as is ordinarily given to orchard and many shade and ornamental trees.

IN FOREST TREES. The means available to the forester in combating decay depend greatly on the character, condition and location of the timber. Even in some virgin stands, the flexibility of modern logging methods may permit a reduction in decay hazard through a preliminary light sanitation cut in which the objective is to work through the forest as rapidly as possible, removing only defective or sporophore-bearing trees and those recognized as likely to succumb to bark beetle attack before the next cutting cycle (162). In parts of the United States, sanitation or improvement fellings are needed on large acreages of cut-over land to remove unmerchantable trees left at the time of original logging because of defectiveness from heart rot (150, 168). The special sanitation felling of trees with sporophores to lessen the danger of infection of the remaining stand, as was instigated by Möeller (221, 222, 268) in Germany against trees bearing sporophores of *Fomes pini,* or of infected trees that could be expected to develop sporophores later (96), undoubtedly has been helpful in reducing the chances for infection in parts of the area covered. Thus Liese (196) states that, as a result of the care given German forests during the last 100 years, heart rots are much less common than in an earlier time.

Under conditions such as reported by Haddow (133) for white pine in Ontario, where most of the sporophore production of *F. pini* was occurring on cull logs left in the woods, felling of the occasional living conk tree would appear to be of little help in reducing chances for infection unless cull material containing the fungus were disposed of also. Hepting and Roth (151), however, as a result of systematic observations on the fruiting of heart-rot fungi on felled cull trees in the Appalachians, found that sporophore production on them was materially less than on comparable unfelled trees, and ceased entirely after ten to 15 years. Therefore, they recommended the felling of such trees. Aoshima (10) urges removal of all dead or down birch as a sanitation measure in forests where heart rot from *Fuscoporia* (*Poria*) *obliqua* is prevalent because this fungus develops sporulating fruit bodies only on dead and down material.

Hepting and Kimmey (150) suggest seven ways in which loss from decay in the United States can be minimized through silvicultural means, where applicable: By adjustment of the cutting age, by avoiding frequent light cuts, by discriminating against defective trees in marking, by special salvage cuts in fire or storm-damaged stands, by control of dwarf mistletoe in species in which mistletoe cankers are common places of entry for decay fungi, by early selective thinning of hardwood stump sprouts and by pruning, or by control of the size of side branches through maintenance of suitable stand density. To these may be added protective measures, such as against fire (125, 144, 149, 215) and wounding by animals, both domestic and wild (116, 136, 144, 254), and silvicultural measures, such as the stimulation of growth through reduced competition, where this can be accomplished without offsetting disadvantages.

For many species for which approximate age-decay relationships in natural stands have been established, financial considerations will probably lead to the cutting of future non-virgin stands before serious losses from heart rots occur. Examples are Douglas-fir (45, 46*a*), Sitka spruce (32), southern pines (146), white-oak (149) and yellow poplar (149). However, species such as aspen (216, 285, 304), balsam fir (175, 207, 301) and scarlet oak (149) will often need to be cut at ages of 50 to 90 years if damaging loss from heart rot is to be avoided, even though larger sizes attained at a greater age might be desired on other grounds. In such species

stimulation of tree growth to the extent feasible under forest conditions would offer a means of offsetting, as far as possible, the size limitations imposed by the necessity for cutting at these relatively early ages.

As pointed out earlier, logging wounds may be an important source of decay, and they affect the potentially most valuable portion of the tree. Haufe (136) has found that, in spruce, wounds from skidding almost invariably lead to extensive and serious decay. Branch and top breakage, felling wounds and butt injury from skidding and yarding increase as the frequency of cutting increases in a given stand (150), especially when logging is by tractor. Obviously, then, the least decay hazard for the residual trees will result when fellings are made as few as practicable, consistent with silvicultural necessities. From this standpoint, clear cutting by blocks or strips is ideal where it can be used.

Among the remaining measures advocated by Hepting and Kimmey, those with the greatest potential significance for heart rot avoidance probably are the selective thinning of stump sprouts and pruning. The danger from butt rot can be very materially reduced by thinning hardwood sprouts before heartwood forms at the base to act as a bridge for decay from the old stump; in thinning operations, low-origin sprouts and those from small stumps should be favored as being less likely to become decayed than those of high origin and from large stumps (144, 273, 275). The pruning of crop trees while the branches are still small, aside from its technical advantages in improving timber quality, is of special benefit in reducing decay hazard in young conifer stands where fungi such as *Polyporus anceps,* which enter through dead side branches, are common (5), although it is also beneficial in hardwoods when done at the proper time (144).

Control of stand density may be useful in several ways in reducing decay hazard: through regulation of branch size (5, 6, 301), in prevention of stagnation (301) and by providing beneficial ground protection (246)—all concerned with the lessening of opportunities for establishment of heart rots. This is apart from the influence of stand density on the growth rate of the trees, which can influence the rate of progress of decays after they have gained entrance, as already noted.

For some types of wounding that provide entrance for heart-rot

fungi, remedies are obvious, but the means of accomplishing them are surrounded with difficulties. Under conditions that exist in India, Bagchee and Bakshi (13) believe that the only possibility for preventing uncontrolled lopping of trees for fodder, bedding material and fuel, which leads to so much decay there, would be by establishment of special fodder and fuel plantations where lopping by the villagers could be concentrated. Similarly, control of debarking of trees by the red deer, a problem that was serious in Saxony prior to World War II, was complicated by an apparent change in the habits of the deer, leading to this form of damage (136), and no means for its prevention had been discovered other than practical destruction of the species as a game animal. What appears to be a similar situation, involving damage from bears in one portion of California (116), has recently been reported.

The butt rot fungi that enter through roots, as *Fomes annosus* often does (157, 262), present a control problem with many facets for which there appears to be no single solution with general applicability, owing to the diversity of conditions that may favor establishment of these fungi. In some situations thinnings or selective cuttings definitely appear to increase the incidence of butt rot in the remaining stand (147, 262) through establishment of the causal fungi in the resulting stumps and subsequent spread into adjacent living root systems; but silviculturally such cutting can hardly be avoided. Prevention of the colonization of the stumps by these fungi may be possible by exhausting the food materials in the stump wood through girdling prior to felling, as demonstrated for *Armillaria mellea* by Leach (192, 193); but, except where labor is very cheap, this method would hardly be financially feasible in forestry. The promising results recently obtained in England by painting freshly cut stump tops with paint or a tar-creosote mixture (260, 263), and experiments in excluding *Fomes annosus* by artificial establishment of the saprophytic decay fungus, *Peniophora gigantea,* in fresh stumps (263), offer interesting possibilities. Other recent experiments that may hold promise in situations where the soil structure favors early infection are the planting of conifer seedlings with the roots spread flat to discourage formation of a tap root, and application of lime or phosphate around conifer bases to discourage attack by *Fomes annosus* (169), although Rishbeth's (261) observations that losses from the fungus are

heavier on alkaline than on acid soils casts some doubt on the chances for success of the latter measures. Fungus competition undoubtedly has a restrictive influence on *Fomes annosus* (35, 260, 261), and means may be found to utilize the demonstrated antibiotic effects of certain soil organisms (35, 255, 259) for control of the disease, but so far these remain in the status of intriguing possibilities. For some conditions under which butt rots are troublesome, conversion to mixed stands is probably still the most practical means of reducing their incidence (110, 246, 254).

IN ORCHARD AND SHADE TREES. Avoidance of heart rots in orchard, shade and ornamental trees rests on three basic principles of action: prevention of wounding wherever possible, prompt treatment and protection of wounds that can not be prevented, and stimulation of growth of the tree to afford as rapid healing as possible (211). Trees for these uses are almost invariably planted, and as some species or varieties, such as the soft maples, ashes and lindens, are much more susceptible to storm or other weather damage than others, the probabilities of future injury may be materially reduced by wise selection of the trees used (290). Selection for functional size to avoid the necessity for heavy future pruning to keep the tree within the space limitations of its location will also reduce future heart-rot hazard. After the tree is planted, intelligent annual pruning to obtain good structural form, prevent overcrowding of branches and provide proper ground, street or sidewalk clearance will reduce the necessity for later removal of large limbs, creating large wounds that are slow to heal (79, 244). The degree of resistance in trees to storm damage can also be increased by pruning with that objective in mind (218). In orchard trees, thinning of fruit, to prevent overloading of branches, and support of limbs bearing heavy fruit loads until the crop is off aid in preventing breaking and splitting down of branches (12, 78).

In parts of the world with definite seasonal temperature differences, wounds made during the spring months usually heal more rapidly than those occurring at other seasons (210), and protective substances are laid down more rapidly then in the sapwood of severed branches than at other seasons (305). However, in some tree species, for example, birch and hard maple, bleeding is more likely to occur from wounds created in early spring than from those made later after the foliage has begun to function (59, 107), caus-

ing difficulties in wound closure and in the adherence of wound dressings.

Smoothing of the wounded surface, particularly if jagged, shaping to favor rapid healing, sterilization of the exposed wood, application of a non-toxic protective coating to the cambial region near the wound edges, and covering the wound with a suitable dressing are recommended measures that greatly reduce the chances for establishment of heart rots (211, 244), although they can not be relied upon to completely prevent decay (339). Wound dressings, none of which is ideal, often need repair or replacement at periodic intervals if their effectiveness is to be maintained (211, 244). Once a heart-rot fungus has become well established, its complete elimination from a tree is ordinarily impracticable because of the penetration that many forms make beyond the limits of visible decay or discoloration (325, 326). Therefore, it appears questionable whether extensive removal of decayed heartwood from a defective tree, as often practiced by arborists (107, 244), serves any effective purposes other than reducing the opportunities for production of fruit bodies of the causal heart-rotting fungus, improving the appearance of the tree, or, as a preliminary to the placement of cavity fillings which provide a foundation over which callus tissue can spread, permitting more rapid natural closure of the opening than would otherwise be possible. Killing or arresting heart-rot fungi through injection of fungicidal or fungistatic materials into affected tree trunks is a possibility that has intrigued many, but which, in actual experimentation, has failed because of the difficulty in obtaining proper diffusion of the injected compound into the affected heartwood.

For the future, perhaps the most promising approach to the development of practical methods for arresting the progress of established heart rots in trees may be through a better understanding of the reasons for the natural arrestment of decay and the dying out of infections that often take place in nature.

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Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

Wood Fiber Length as Related to Position in Tree and Growth	Stephen H. Spurr *University of Minnesota*
Compression Wood in Conifers as a Morphogenetic Phenomenon	
Seed Germination Problems in the Umbelliferae	Richard Robinson *University of California*
The Cryptogamic Flora of the Arctic:	
Algae	William Randolph Taylor *University of Michigan*
Algae: Planktonic groups	R. Ross *British Museum, London*
Bacteria	C. D. Kelly *McGill University*
Bryophytes	William Campbell Steere *Stanford University*
Fungi	Rolf Singer *Farlow Herbarium, Cambridge*
Lichens	Eilif Dahl *Yale University*
On Modified Hyphae of Hymenomycetes	Paul L. Lentz *U. S. Bureau of Plant Industry*
Cytogenetics of the Vegetable Crops. I. Monocotyledons	S. H. Yarnell *U. S. Department of Agriculture*
The Morphology of Leaves	Vera L. Ryder *Oregon State College*
In Vitro Culture of Plant Embryos and Factors Controlling Their Growth	Jaques Rappaport *University of Virginia*
Ecological Processes and Vegetation of the Maritime Strand in the Southeastern United States	Henry J. Oosting *Duke University*
Some Historical Chapters on Tree Growth	R. A. Studhalter *Texas Technological College*
The Shoot Apex in Angiosperms	Ernest M. Gifford, Jr. *University of California*
Growth Rings and Climate	Waldo S. Glock *Macalester College*
Apomixis in the Angiosperms. II.	Axel Nygren *Agricultural College of Sweden*